THE EFFECTS OF MARSH EDGE AND SURFACE ELEVATION ON THE DISTRIBUTION OF SALT MARSH INFAUNA AND PREY AVAILABILITY FOR NEKTON PREDATORS

A Thesis

by

SHANNON DIANN WHALEY

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

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Major Subject: Wildlife and Fisheries Sciences

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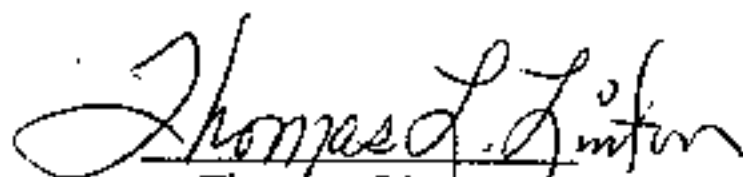
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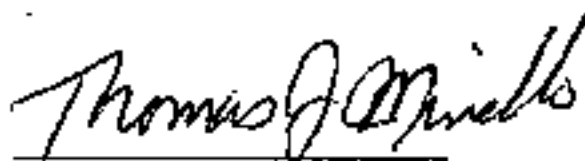
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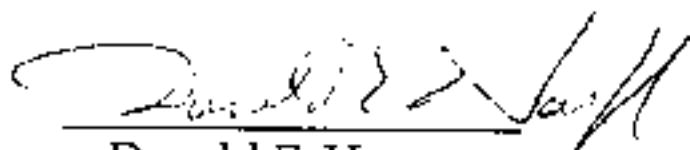for the degree of

MASTER OF SCIENCE

Approved as to style and content by:

Thomas Linton
(Co-Chair of Committee)

Thomas J. Minello
(Co-Chair of Committee)

Donald E. Harper
(Member)

Robert Brown
(Head of Department)

December 1997

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

The Effects of Marsh Edge and Surface Elevation on the Distribution of Salt

Marsh Infauna and Prey Availability for Nekton Predators. (December 1997)

Shannon DiAnn Whaley, B. S., Texas A&M University

Co-Chairs of Advisory Committee: Dr. Thomas Linton
Dr. Thomas Minello

The relative importance of edge and elevation on infaunal distribution patterns within an intertidal <u>Spartina</u> <u>alterniflora</u> salt marsh was examined by collecting infauna on the nonvegetated intertidal and within the marsh at distances of one, three, five, and ten meters from the marsh edge. During most of the year, densities of most polychaetes and crustaceans within marsh vegetation were highest one meter from the marsh edge compared with densities farther from the marsh edge. Distributions of surface-dwelling infauna had the strongest relationship with marsh edge; whereas, some subsurface feeders were not affected by proximity to edge. Multivariate analysis of covariance suggested that densities of overall infauna were consistently related to marsh edge throughout the year even after accounting for elevation effects. The relationship between infaunal abundance and surface elevation was significant only during the early spring, mid-summer, and late fall. These data suggest that edge effects influence infaunal distributions more than elevation within the salt marsh.

The relative value of the marsh surface and associated intertidal infaunal populations to predators was examined in two laboratory experiments (in May and August, 1995). Growth comparisons were made of several common marsh

predators such as brown shrimp (<u>Penaeus aztecus</u>), white shrimp (<u>Peneaus setiferus</u>), and gulf killifish (<u>Fundulus grandis</u>) that were allowed to forage for two weeks on sediments from three different microhabitats: nonvegetated intertidal, marsh one meter from the edge, and marsh ten meters from the edge. Growth rates were not significantly different among microhabitats, but in each experiment, growth rates were less than those reported in the literature for wild populations. Thus, predator growth appeared to be food-limited in experimental chambers, and growth rates were not an accurate measure of microhabitat value.

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I am grateful to many employees of the National Marine Fisheries Service Galveston Laboratory who cheerfully helped me with field sample collections and laboratory experiments.

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Dr. Lawrence Rozas, Dr. Teresa McTigue, and Dr. Pete Sheridan also contributed to my success by offering much appreciated advice at all stages of this study. Their vast knowledge in the areas of experimental design and applied estuarine ecology enriched this study and my life as a graduate student.

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CHAPTER I

INTRODUCTION

The marsh surface is valuable to transient and resident natant species as a source of food. Many of these natant organisms prey on infauna that are abundant in vegetated intertidal salt marshes (Weisberg and Lotrich 1982; Zimmerman et al. 1991). Although these infaunal prey populations are an important link in the marsh ecosystem, their spatial and temporal patterns within the intertidal zone have not been adequately described. Among the many physical and biological factors regulating intertidal infaunal populations, surface elevation and hydroperiod appear to play a dominant role (Subrahmanyam and Coultas 1980; Moy and Levin 1991). Elevation in conjunction with hydroperiod can affect sediment characteristics (Stumpf 1983; Warren and Niering 1993), pore water salinity (Morris et al. 1990; Warren and Niering 1993), vegetation patterns (Mendelssohn and Seneca 1980; McKee and Patrick 1988; Reed and Cahoon 1992), and desiccation (Hummel et al. 1986). Zimmerman et al. (1991) found that marsh infaunal populations were also influenced by intense predation pressure at certain times of the year. Intertidal areas near the marsh-open water interface may be more accessible to predators, and predators have been found to concentrate in these areas (Baltz et al. 1993; Kneib and Wagner 1994; Minello et al. 1994; Peterson and Turner 1994). Thus, predation pressure could be higher near the marsh edge compared with the inner marsh. In turn, infaunal populations found near the marsh edge may be a more valuable food source to these predators (Minello et al. 1994).

This thesis follows the format of the journal Estuaries.

The first objective of this study was to investigate the relationships between marsh edge, surface elevation, and hydroperiod and on intertidal infaunal abundance in a Texas salt marsh. The study site consists of several sections of an intertidal _Spartina alterniflora_ marsh. Marsh sections were selected that had a distinct edge and variability in slope. In addition, all sections were characterized by monospecific stands of _Spartina alterniflora_ that extended landward at least 20 m in from the marsh edge. Infaunal populations were sampled along transects running parallel to the marsh edge. Elevations at each sample site were measured to examine the effect of elevation within transects. Abundance patterns were interpreted with respect to seasonal abundance of nektonic predators and hydroperiod. This field study was designed to test the null hypothesis that distance to the edge and elevation were unrelated to infaunal abundance in the intertidal salt marsh.

The second objective of this investigation was to examine the relative value of the marsh surface and associated intertidal infaunal populations for some common salt marsh predators. This objective was accomplished by measuring growth of predators under controlled laboratory conditions. Intact sediment was taken from the intertidal marsh in experimental chambers at fixed distances from the marsh edge and placed in a laboratory water table. Bringing the sediment cores into the laboratory allowed me to make microhabitats equally available to predators. Common marsh nektonic predators were allowed to feed within the chambers, and relative value of the marsh surface was determined by comparing the growth of these predators in the different treatments. Growth experiments were conducted in the spring and summer to explore the possibility of seasonal

variations. These controlled laboratory experiments were designed to test the null hypothesis that at different distances from the edge, intertidal marsh surfaces and their associated biota have similar value to nekton predators.

CHAPTER II

LITERATURE REVIEW

The benthic infaunal community is a significant link in the salt marsh ecosystem. This ecosystem receives energy not only from macrophytic primary production in the form of detritus but also from benthic and epiphytic algae (Odum 1980; Tenore et al. 1982, Schwinghamer et al. 1991). Energy from these sources is passed on to the intertidal benthic community (Tenore et al. 1982). Benthic infauna, as prey, transfer energy to many natant predators who use the intertidal marsh surface as a source of food (Kneib and Stiven 1978; Weisberg and Lotrich 1982; Thomas et al. 1990; Zimmerman et al. 1991). The abundance of these infaunal populations, and their accessibility to predators are major factors in determining the overall productivity of a coastal salt marsh (Zimmerman et al. 1991).

Infaunal abundance patterns in the dynamic habitat of the intertidal salt marsh are probably influenced by many factors (Woodin 1974; Bell et al. 1978; Bell 1979; Subrahmanyam and Coultas 1980). One prominent and unique characteristic of the intertidal zone is the continuous changing from aquatic to terrestrial habitat. This process is governed by the hydroperiod and the topography of the intertidal area. The frequency and duration of tidal inundation is distinctive for marsh areas at different elevations. Therefore, small differences in elevation can lead to very different hydroperiods for the biotic components living in various microhabitats within the intertidal zone. In addition, the distance from the marsh edge may also have a profound effect on intertidal habitat conditions (Minello et al. 1994). Elevation and distance to the marsh-open water interface have

been proposed as important factors controlling marsh use and value for organisms at many trophic levels including commercially important natant species such as shrimp and blue crabs as well as benthic infauna (Zimmerman and Minello 1984; Childers et al. 1990; Minello et al. 1994). These two characteristics, in conjunction with the area's hydroperiod, control infaunal communities directly and indirectly by affecting many physical and biological processes occurring in the intertidal zone.

Elevation and distance to the marsh edge influence infaunal communities by creating soil zones within the intertidal marsh (Warren and Niering 1993), controlling the extent of desiccation (Hummel et al. 1986), and affecting vegetation density and type. Although animal-sediment relations in tidal marshes are not well understood, sediment characteristics are thought to influence infaunal abundance (Van Dolah 1978; Hummel et al. 1986; Warren and Niering 1993). Generally, as elevation and distance from the edge increase, sediment particle size becomes smaller (Stumpf 1983), sediment drainage decreases (Yelverton and Hackney 1986), and soil water salinity increases (Morris et al. 1990; Warren and Niering 1993). In studies of infaunal communities in deeper, subtidal habitats, sediment grain size was found to be the primary factor controlling species composition (Johnson 1970; Flint and Kalke 1985; Swift 1993). In addition, sediment characteristics, such as the amount of organic matter, appear related to the development of intertidal benthic communities in created salt marshes (Sacco 1989; Minello and Zimmerman 1992). Warren and Niering (1993) have suggested that sediment drainage characteristics and soil water salinity are important in controlling intertidal communities in salt marshes. In addition to sediment characteristics, surface elevation also controls the

extent and duration of desiccation that a particular area and its associated infaunal community must endure. In the Dutch Oosterschelde estuary in the Netherlands, Hummel et al. (1986) found that prolonged desiccation at higher elevations of the intertidal salt marsh when combined with high temperatures greatly increased infaunal mortality rates. Therefore, declines in infaunal abundance might be expected at higher elevations in the warmer months of the year. Another important characteristic that is believed to influence infaunal abundance is vegetation density (Rader 1984; Lana and Guiss 1991). Vegetation stem density in the intertidal zone has been found to increase with increasing elevation and decreasing hydroperiod (Mendelssohn and Seneca 1980; McKee and Patrick 1988, Reed and Cahoon 1992). Vegetation density can affect intertidal communities in several ways such as altering organic matter levels in the sediment (Lana and Guiss 1991), or controlling the amount of oxygenated habitat (Teal and Kanwisher 1966).

Biological factors influencing infaunal abundance are also affected by elevation and distance to the marsh edge. Zimmerman et al. (1991) indicated that predation has a great effect on intertidal infauna abundance at certain times of the year when predators are most abundant in the marsh. Studies conducted in several different geographic locations on the Atlantic and Gulf coasts found similar inverse relationships between seasonal abundance of natant predators and infauna (Cammen 1976; Bell 1979; Subrahmanyam and Coultas 1980; Kneib and Stiven 1982; Zimmerman et al. 1991). This correlation suggests that predation pressure is a prevalent influence on marsh infaunal abundance in many areas. Elevation and hydroperiod control the availability of intertidal prey to predators. The

distance from the marsh edge can also limit predation. Areas very close to the marsh edge (near open water) may be more accessible than inner marsh areas due to the structural complexity of the roots and stems of intertidal marsh vegetation. Several studies have found that at high tide, when the entire intertidal habitat was available, more natant predators were found in areas nearest to the edge than the inner marsh (Kneib and Wagner 1994; Minello et al. 1994; Peterson and Turner 1994). One can infer from these studies that predation pressure is more frequently a controlling force in areas of low elevation due to regular flooding, and a more significant force near the marsh edge as a result of greater predator accessibility. Predation pressure, as a biological factor potentially affecting infaunal abundance, has received the most attention by researchers. Not much is known about the influence on the salt marsh intertidal community of such biological factors as competition and larval settlement. The occurrence of competition in the intertidal zone of the salt marsh is thought to be infrequent because community densities are believed to be below carrying capacity (reviewed by Peterson 1979). Larval settlement, however, can influence intertidal populations in marshes (Woodin 1974; Bell 1979), and settlement may also be affected by the distance from the marsh edge and the surface elevation. Many species of benthic infauna found in the marsh have planktonic larvae. Just as marsh edge and surface elevation limit accessibility for natant predators, these larva may also be restricted to settling in areas near the edge and at lower elevations. More research is needed to clarify the relationships between topography of the intertidal zone and biological factors affecting the intertidal community of the salt marsh.

Several studies have contributed limited insight into edge and elevation effects on intertidal infaunal abundance. In the northern Gulf of Mexico, Minello et al. (1994) tested for the effect of marsh edge on use of natant predators in a created salt marsh. In that study, a limited number of benthic infaunal samples were also taken, and infaunal densities were significantly higher 1-2 m away from the marsh edge than in the inner marsh approximately 35 m away from the nearest edge. On Sapelo Island, Georgia, Kneib (1984) also found that densities of infauna decreased as distance from the edge increased. In this study, highest densities were detected within 25 meters of the marsh edge. Both Kneib (1984) and Minello et al. (1994) found that, Streblospio benedicti, a common infaunal polychaete, decreased in abundance as distance from the edge increased. In North Carolina, Moy and Levin (1991) also observed that abundance of this species generally decreased as the elevation increased, although distribution patterns fluctuated temporally and were occasionally inconsistent. Subrahmanyam and Coultas (1980) found that the intertidal infaunal community structure in two north Florida marshes consisted of three distinct groups; group occurrence depended on elevation. These studies imply that edge and elevation are important in determining infaunal abundance and community structure, but there is little information on how each factor individually affects the benthic community. An examination of the individual effects of marsh edge, elevation, and associated hydroperiod is needed to begin to understand the relationships among these physical factors and the intertidal infaunal community.

Benthic infauna found in salt marsh sediments provide an important food source for many natant predators. Weisberg and Lotrich (1982) found

that intertidal marsh surfaces were much more valuable than subtidal areas for one natant predator, <u>Fundulus</u> <u>heteroclitus</u>. Growth rates for this species were significantly higher when allowed access to intertidal marsh surfaces. In a similar experiment, Minello and Zimmerman (1991) found that brown shrimp (<u>Penaeus</u> <u>aztecus</u>) in cages with access to vegetated marsh surfaces also grew faster than those in cages that confined them to nonvegetated subtidal bottom. These results are consistent with findings of higher prey abundance on the marsh surface compared to subtidal areas (Rader 1984; Lana and Guiss 1991; LaSalle and Rozas 1991; Zimmerman et al. 1991). Although the intertidal zone of the salt marsh is known to be valuable to predators, microhabitats within this zone may differ in value. At times when the entire intertidal habitat was available, Peterson and Turner (1994) found that predators were concentrated in areas near the marsh edge. One explanation proposed for this high predator concentration was a possible increase in food value in areas near the edge (Minello et al. 1994). To examine this possibility further, a growth study is needed to compare the relative value of microhabitats within the intertidal salt marsh for predators that use the marsh surface as a source of food.

CHAPTER III

THE DISTRIBUTION OF BENTHIC INFAUNA IN RELATION TO MARSH EDGE AND SURFACE ELEVATION

Introduction

Elevation, in conjunction with tidal inundation, influences the zonation of benthic organisms in both soft-bottom intertidal and rocky intertidal habitats (Dayton 1971; Vermeij 1972; Menge 1976; Subrahmanyam and Coultas 1980; Kneib 1984; Posey 1986; Miron and Desrosiers 1990; Caron et al. 1996; McLachlan 1996). Hummel et al. (1986, 1994) found that elevation and flooding duration influence the survival and distribution of benthic organisms within the intertidal salt marsh, and relationships between elevation and infauna distribution have been well-documented (Cammen 1976; Subrahmanyam et al. 1976; Subrahmanyam and Coultas 1980; Fell et al. 1982; Subrahmanyam 1984; West and Williams 1986; Bishop and Hackney 1987; Peterson and Black 1988; Moy and Levin 1991; Kneib 1992; Stiven and Gardner 1992). However, proximity to the marsh-open water interface (marsh edge) has also been suggested as potentially important in controlling distribution patterns (Kneib 1984; Lin 1990; Minello et al. 1994). Edge effects have rarely been considered a possible influence on infaunal distribution within the marsh, and the few studies that have considered edge effects have not been able to differentiate between the effects of elevation and edge because these factors are generally confounded.

There is some evidence from the Galveston Bay System that distance to the marsh edge may have an effect on infauna distribution independently of elevation. Minello et al. (1994) tested for the effect of marsh edge on predator use of a created salt marsh and collected a limited number of benthic infauna samples. With elevations held constant, densities of infauna and nekton were significantly higher 1-2 m away from the marsh edge than in the inner marsh approximately 35 m away from the nearest edge.

Elevation probably influences infauna distribution by creating a gradient of varying habitat conditions along the slope of the intertidal salt marsh. By affecting the duration and frequency of tidal flooding and desiccation, elevation affects temperature (Hummel et al. 1986), sediment drainage (Yelverton and Hackney 1986, Harvey et al. 1987), pore water salinity (Morris et al. 1990; Warren and Niering 1993) and vegetation patterns (Mendelssohn and Seneca 1980; McKee and Patrick 1988; Reed and Cahoon 1992). Elevation has often been positively correlated with vegetation density and sediment organic levels and these factors appear important to infaunal distribution patterns (Rader 1984; Sacco 1989; Lana and Guiss 1991). Vegetation stem density in the intertidal zone has been found to increase with increasing elevation and decreasing hydroperiod (Mendelssohn and Seneca 1980; McKee and Patrick 1988, Reed and Cahoon 1992). In contrast, production rates of Spartina alterniflora appear to be higher at low elevations where the tall form grows (Squiers and Good 1974), and densities of some infaunal species such as the ribbed mussel (Geukensia demissa) have been positively correlated with these production rates (Fell, et al. 1982).

Marsh edge may influence the distribution of infauna by affecting predation pressure, and the settlement of sediment, planktonic larva, and suspended food particles along the intertidal gradient. Predation pressure may be higher near the marsh edge because nektonic predators have been found to concentrate in these areas (Baltz et al. 1993; Kneib and Wagner 1994; Minello et al. 1994; Peterson and Turner 1994). Sediment deposition is also higher near the marsh edge. As water flows across the marsh surface, marsh vegetation slows water velocity causing the majority of suspended sediments to settle out of the water column within several meters of the marsh edge (Stumpf 1983; Warren and Niering 1993; Jadhav and Buchbergereco 1995). In a similar way, marsh vegetation may also facilitate the settlement of planktonic infaunal larvae and suspended food particles in areas near the marsh edge.

Analysis of the relative importance and potential seasonality of elevation and edge effects is useful in understanding mechanisms controlling population dynamics within marsh systems. The purpose of this study is to explore the relationships between edge, elevation, and the distribution of benthic infauna in a Texas salt marsh. Elevation and edge effects were examined by sampling benthic infauna within a Spartina alterniflora salt marsh every six weeks for a year. Infaunal populations were sampled in five microhabitats represented by transects running parallel to the marsh edge. Marsh slopes varied and therefore elevations varied within transects.

Methods

Collection of Marsh Infauna and Sediment Samples

The study area was located in a natural marsh located on Gang's Bayou in Galveston Bay, TX (Figure 1). This polyhaline <u>Spartina alterniflora</u> marsh is located on the west end of Galveston Island at a latitude of 29° 15' 22" N and a longitude of 94° 55' 03" W. The sampling area covered 1000 m of shoreline and included several sections of the marsh's intertidal zone that had different slopes. I sampled benthic infauna within these sections of the marsh every six weeks in 1995. Samples were taken along five transects oriented parallel to the shoreline. Each transect represented a microhabitat. The lowest-elevation transect was positioned on the nonvegetated mudflat, one meter away from the marsh edge. Remaining transects were placed within marsh vegetation at successively greater distances from the marsh edge (1, 3, 5, 10 m away). Because marsh slope was variable, elevation of the marsh surface varied within transects. The elevation at each sampling site was determined by measuring the water level at the time the sample was collected and comparing this level to a permanent water level gauge in Gang's Bayou. With the exception of the February 22nd collection, sampling occurred at high tide so that the entire intertidal zone was inundated and water level for all sites could be recorded. In February, tides were rarely high enough to cover the entire marsh. Therefore, samples were taken with the marsh exposed and sample sites marked by stakes. Elevations of these sites were measured three weeks later when tides were high enough to cover the entire marsh surface.
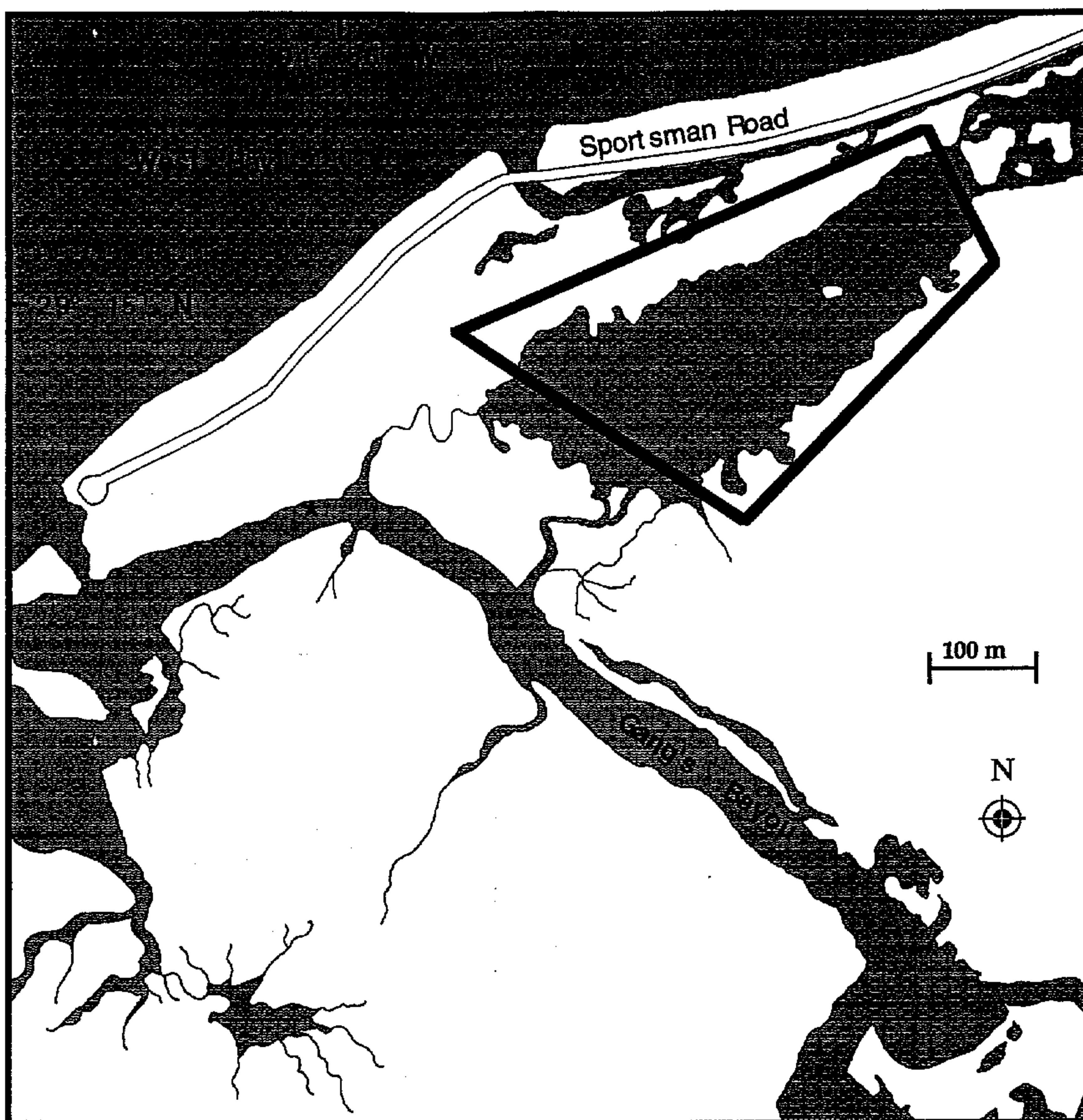
Figure 1.   Map of sampling area located near Gang's Bayou.
This area is off West Bay in the Galveston Bay System of Texas.
The area within black lines contains the 1000 meters of shoreline
that was sampled in this study. Asterisk indicates location of
water level recorder.

Water levels were recorded every hour for the duration of the study using a water level recorder (Remote Data Systems WL40™) installed near the sampling area (Figure 1). Unfortunately, extremely high water levels caused by Hurricane Opal damaged our water level recorder. After October 4th, water level data were extrapolated from water levels measured at a NOAA tide station (No. 887-1450) in the Galveston Ship Channel (29° 18.6' N and 94° 47.6' W) approximately 12.5 kilometers from the sample site. The relationship between water levels at the sample site and tide station was determined by using data from April to August, 1995 (marsh level = .539*(tide station)-17.080cm, r=0.634). Water temperature and salinity in the sampling area were measured hourly by a Hydrolab Datasonde located next to the water level recorder in Gang's Bayou. Sediment temperatures were recorded every hour using small temperature loggers placed in air-tight containers and positioned 1 cm below the sediment surface in three microhabitats: nonvegetated (-1 M), 1 M, and 10 M from the marsh edge. Daily mean air temperatures were obtained from a NOAA weather station (No. 12923) located at Scholes Field Air Base (29° 18' N and 94° 48' W) in Galveston.

Every six weeks, I collected 25 infaunal sediment cores (5-cm diameter to a depth of 5 cm) at random sites along each of the five transects (125 samples total). I established the number of samples by examining similar infauna data taken in a near-by marsh. Twenty-five samples per transect should allow detection of at least a 50% difference in transect means (Sokal and Rohlf 1981). Vegetation in the coring area was quantified and snipped off at the mudline to preclude epiphytic organisms from the sample. During the first sampling period in February, two additional sediment cores

(3-cm diameter, 5 cm depth) were taken per sample site to characterize sediment grain size and organic content (SOC) for microhabitats. All cores were placed in plastic bags and stored on ice.

In the laboratory, benthic infaunal cores were sieved through a 500-µm mesh and preserved in 10% formalin with rose bengal stain. Annelids, small crustaceans, and mollusks from the infaunal sample were counted and identified to species or to the lowest feasible taxonomic level, dried at 100°C for 24 hours, then weighed. The amount of macroorganic matter (MOM) in each of the microhabitats was determined using infauna sediment cores from the July collection. Once the samples were sieved through a 500-µm mesh sieve and infaunal organisms were removed, material which appeared to be living at the time of collection (LMOM) was separated from detritus (DMOM) under a dissecting microscope. This material was oven-dried for 24 hours at 100°C and weighed to determine dry biomass. Sediment organic content (SOC) was determined by the ignition loss method (Dean 1974). SOC sediment cores were wet sieved through a 2-mm mesh to remove stems and roots, air-dried under a vacuum hood to remove most of the water, ground with mortar and pestle, placed in pre-weighed ceramic crucibles and dried at 110°C for 24 hours to remove any remaining interstitial water. Samples were transported in a desiccation chamber to be weighed, burned in a muffle furnace at 375°C for four hours, cooled in a desiccation chamber, and re-weighed. Sediment grain size was analyzed using the sieving and pipette techniques described by Folk (1980). I sampled sediment grain size and organic content (February), and below-ground macroorganic material (July) only once during the year because

these sediment characteristics remain relatively constant on an annual time scale in well-established natural marshes (Whitlatch 1981).

Statistical Analyses

Infaunal abundance data were analyzed using the SuperANOVA statistical package (Abacus Concepts, Inc., Berkeley, CA, 1989), after being transformed using a $L_n(y+1)$ transformation in order to meet assumptions of analysis of variance (ANOVA). I used a one-way ANOVA to test for differences among microhabitats (transects) for each sampling period in order to describe the patterns of infaunal abundance in relation to the marsh edge. Separate analyses were conducted for total infauna, overall polychaetes, Capitella capitata, Streblospio benedicti, Laeonereis culveri, oligochaetes, and crustaceans; the Sequential Bonferroni technique, as described by Rice (1988), was used to adjust significant levels for multiple tests. I used *a priori* linear contrasts to make comparisons among microhabitats.

The relative contribution of distance to the edge and elevation on infaunal distribution in the marsh cannot be determined from ANOVA results. Therefore, multivariate analysis of covariance (MANCOVA), using Wilks' lambda, was used to determine the relative importance of edge and elevation effects on distribution patterns within the marsh. When the covariate, elevation, was not significant (p value > 0.05) in preliminary tests, I applied multivariate analysis of variance (MANOVA) to test for edge effects.

Results

General Distribution of Benthic Infauna among Microhabitats

Polychaete (51.7 %) and oligochaete (32.5 %) worms and peracarid crustaceans (14.5 %) dominated benthic infauna from sediment cores (Table 1). Abundances varied temporally through the year and spatially among microhabitats, and highest abundances generally occurred in the winter and early spring, with low densities during August through October (Figures 2-8). The most abundant polychaetes in samples were surface deposit feeders and suspension feeders. These two feeding groups dominated the marsh edge microhabitat by making up 55% of all annelids, crustaceans, and mollusks found on the marsh edge (Table 1). Subsurface deposit feeders dominated areas three (65%), five (74%), and ten (83%) meters from the marsh edge. The nonvegetated microhabitat had similar numbers of surface (43%) and subsurface (43%) deposit feeders. Omnivorous species accounted for 14% of the organisms in the nonvegetated area, but only from 5 to 7% within marsh microhabitats. Species richness was similar among the microhabitats.

During spring and early summer, densities of benthic infauna within vegetation were generally highest near the marsh edge (Figure 2, Table 2). However, as densities declined in summer and early fall, differences among microhabitats were reduced; by October there were few significant differences in density among the five microhabitats (Table 2). In early spring, densities on nonvegetated bottom were relatively high, and not significantly different from densities in marsh edge habitat. However,

Table 1. Density and biomass of benthic infauna (per 19.6-cm^2 core) in cores collected along five transects: 1 meter downslope of marsh edge in a nonvegetated area (-1M), and within the marsh at distances of 1 M, 3 M, 5 M, and 10 M from the edge in Gang's Bayou. Annual means and standard errors (SE) are calculated from 175 cores collected at each of the five transects over all seven sampling periods throughout the year of 1995. Feeding mode was determined for annelids, crustaceans, and mollusks according to Bousfield (1973), Andrews (1981), and Heard (1982): DD = direct deposit feeders (subsurface), Su = suspension feeder, SD = surface deposit feeder, O = omnivore, C=carnivore.

Distance from the Marsh Edge:	Feeding Mode	-1 M Mean	(SE)	1 M Mean	(SE)	3 M Mean	(SE)	5 M Mean	(SE)	10 M Mean	(SE)	TOTAL Abundance
Total Infauna		31.99	(1.98)	63.23	(5.17)	32.44	(2.42)	26.91	(1.95)	26.20	(1.82)	31635
Annelida		27.56	(1.64)	46.45	(3.05)	28.57	(2.12)	24.94	(1.80)	24.76	(1.74)	26649
Polychaeta		23.10	(1.38)	34.04	(2.52)	15.51	(1.48)	11.37	(1.20)	9.43	(0.88)	16356
Capitella capitata	DD	8.59	(0.74)	11.90	(0.94)	7.75	(0.77)	6.14	(0.73)	5.69	(0.57)	7012
Streblospio benedicti	SuSD	8.89	(0.84)	17.33	(1.76)	5.19	(0.77)	3.06	(0.51)	1.86	(0.30)	6358
Laeonereis culveri	O	4.49	(0.41)	3.41	(0.39)	1.53	(0.25)	1.70	(0.26)	1.50	(0.22)	2208
Sabella sp.	Su	0.13	(0.04)	0.75	(0.27)	0.84	(0.27)	0.31	(0.07)	0.26	(0.09)	401
Leitoscoloplos foliosus	DD	0.54	(0.12)	0.03	(0.02)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	101
Neanthes succinea	C	0.07	(0.02)	0.23	(0.05)	0.09	(0.03)	0.11	(0.04)	0.08	(0.03)	100
Polydora ligni	SD	0.14	(0.04)	0.25	(0.12)	0.05	(0.02)	0.02	(0.01)	0.01	(0.01)	80
Melinna maculata	SD	0.12	(0.03)	0.10	(0.03)	0.05	(0.02)	0.03	(0.02)	0.04	(0.02)	59
Heteromastus filiformis	DD	0.08	(0.02)	0.01	(0.01)	0.01	(0.01)	0.00	(0.00)	0.00	(0.00)	17
Marphysa sanguinea	C	0.00	(0.00)	0.02	(0.01)	0.01	(0.01)	0.01	(0.01)	0.00	(0.00)	6
Scoloplos fragilis	DD	0.03	(0.02)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	5
Mediomastus sp.	DD	0.02	(0.01)	0.00	(0.00)	0.01	(0.01)	0.00	(0.00)	0.00	(0.00)	4
Arenicola cristata	DD	0.01	(0.01)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	2
Eteone heteropoda	C	0.00	(0.00)	0.01	(0.01)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	2
Scolelepis texana		0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.01	(0.01)	0.00	(0.00)	1
Oligochaeta	DD	4.46	(0.50)	12.41	(1.30)	13.06	(1.11)	13.57	(1.08)	15.33	(1.37)	10293
Crustacea		4.31	(0.65)	16.15	(2.98)	3.33	(0.56)	1.54	(0.29)	0.83	(0.15)	4579
Hargeria rapax	SD	0.72	(0.13)	10.33	(2.07)	2.19	(0.38)	0.86	(0.24)	0.38	(0.08)	2535
Corophium sp.	SD	2.59	(0.46)	4.93	(1.43)	0.62	(0.24)	0.24	(0.07)	0.13	(0.05)	1489
Gammarus mucronatus	SD	0.18	(0.05)	0.50	(0.10)	0.41	(0.07)	0.39	(0.07)	0.29	(0.06)	310
Ampelisca sp.	SuSD	0.40	(0.33)	0.16	(0.09)	0.02	(0.01)	0.02	(0.01)	0.01	(0.01)	108
Grandidierella bonnieroides	SD	0.29	(0.09)	0.14	(0.04)	0.04	(0.02)	0.02	(0.01)	0.02	(0.01)	88
Cl. Copepoda	Su	0.09	(0.03)	0.08	(0.04)	0.03	(0.03)	0.01	(0.01)	0.00	(0.00)	36
Mysidopsis bahia	SD, C	0.03	(0.02)	0.00	(0.00)	0.01	(0.01)	0.00	(0.00)	0.00	(0.00)	6
O. Cladocera	Su	0.00	(0.00)	0.02	(0.01)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	3
Edotea montosa		0.02	(0.01)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	3
F. Caprellidae		0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.01	(0.01)	0.00	(0.00)	1
Mollusca		0.05	(0.02)	0.14	(0.05)	0.10	(0.05)	0.10	(0.03)	0.08	(0.02)	82
Cerithidea pliculosa	SD	0.05	(0.02)	0.05	(0.02)	0.03	(0.01)	0.07	(0.03)	0.08	(0.02)	49
F. Hydrobiidae	SD	0.00	(0.00)	0.05	(0.05)	0.06	(0.05)	0.02	(0.01)	0.00	(0.00)	22
Geukensia demissa	Su	0.00	(0.00)	0.04	(0.02)	0.01	(0.01)	0.01	(0.01)	0.00	(0.00)	10
Chione cancellata	Su	0.00	(0.00)	0.01	(0.01)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	1
Nudibranchia		0.00	(0.00)	0.01	(0.01)	0.01	(0.01)	0.00	(0.00)	0.00	(0.00)	3
Number of Species		20		19		18		16		13		29
Other		0.07	(0.02)	0.48	(0.12)	0.45	(0.07)	0.33	(0.07)	0.53	(0.14)	325
Insect larvae		0.05	(0.02)	0.39	(0.11)	0.39	(0.07)	0.32	(0.07)	0.51	(0.14)	291
Nemertea		0.02	(0.01)	0.03	(0.02)	0.02	(0.01)	0.01	(0.01)	0.01	(0.01)	14
Fish larvae		0.01	(0.01)	0.03	(0.02)	0.01	(0.01)	0.01	(0.01)	0.01	(0.01)	11
Hydrozoa		0.00	(0.00)	0.02	(0.02)	0.01	(0.01)	0.00	(0.00)	0.00	(0.00)	5
Turbellaria		0.00	(0.00)	0.00	(0.00)	0.01	(0.01)	0.00	(0.00)	0.00	(0.00)	1
Infaunal Biomass		6.59	(0.60)	7.80	(1.81)	3.22	(0.40)	2.30	(0.26)	1.91	(0.22)	3893.20
Annelid Biomass (mg)		5.88	(0.56)	6.79	(1.79)	2.78	(0.38)	1.93	(0.25)	1.72	(0.21)	3412.70
Crustacean Biomass (mg)		0.51	(0.12)	0.82	(0.14)	0.30	(0.05)	0.17	(0.03)	0.08	(0.02)	330.50
Other Biomass (mg)		0.21	(0.17)	0.19	(0.05)	0.14	(0.03)	0.21	(0.06)	0.11	(0.03)	150.00

Figure 2.   Mean densities of all infauna in the five microhabitats for each sampling date. Each mean represents data from 25 sediment cores; error bars indicate one standard error. Each core had a surface area of 19.6 cm² and a depth of 5 cm.
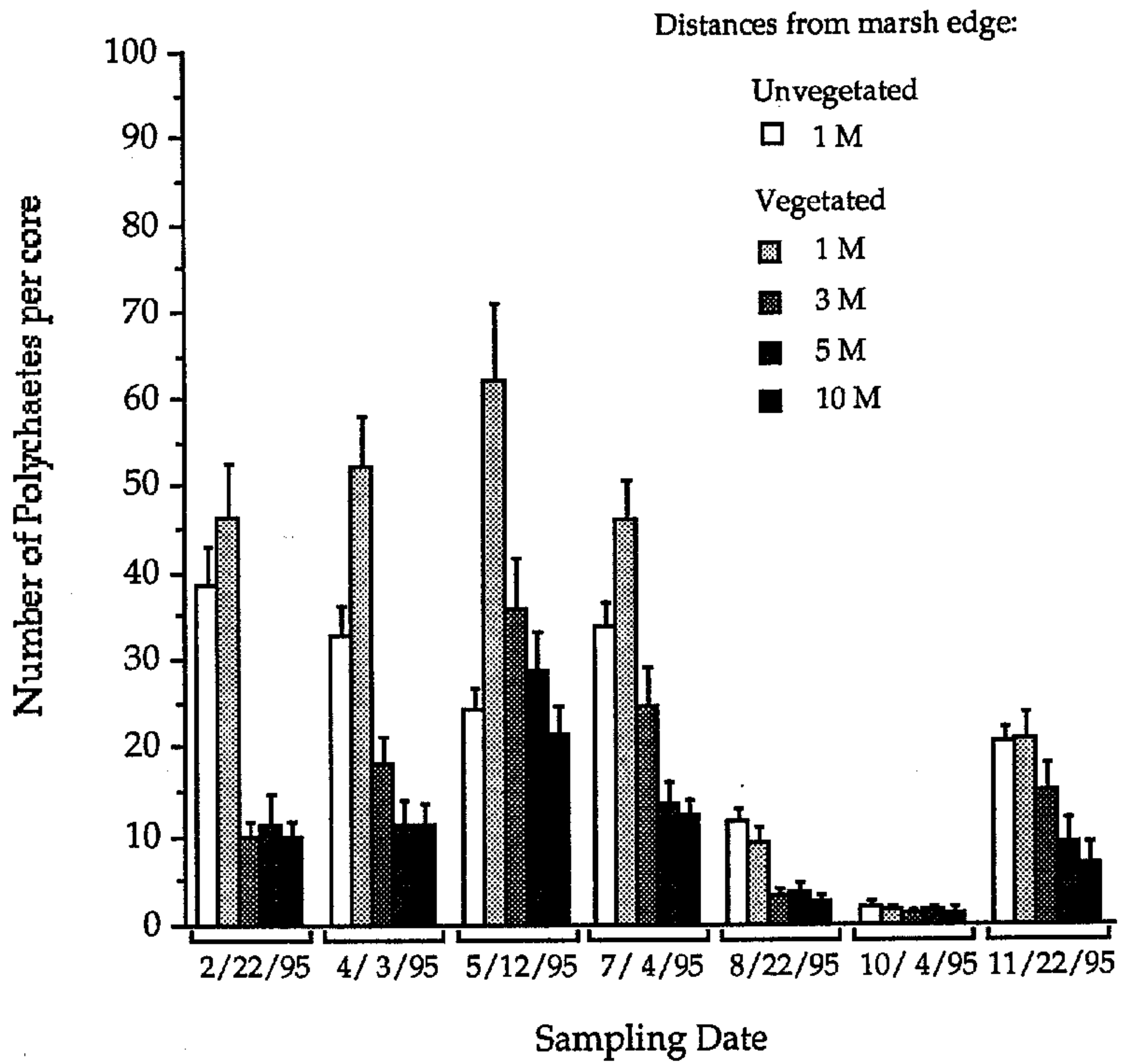
Figure 3.   Mean polychaete densities in the five microhabitats for each sampling date. Each mean represents data from 25 sediment cores; error bars indicate one standard error. Each core had a surface area of 19.6 cm^2 and a depth of 5 cm.
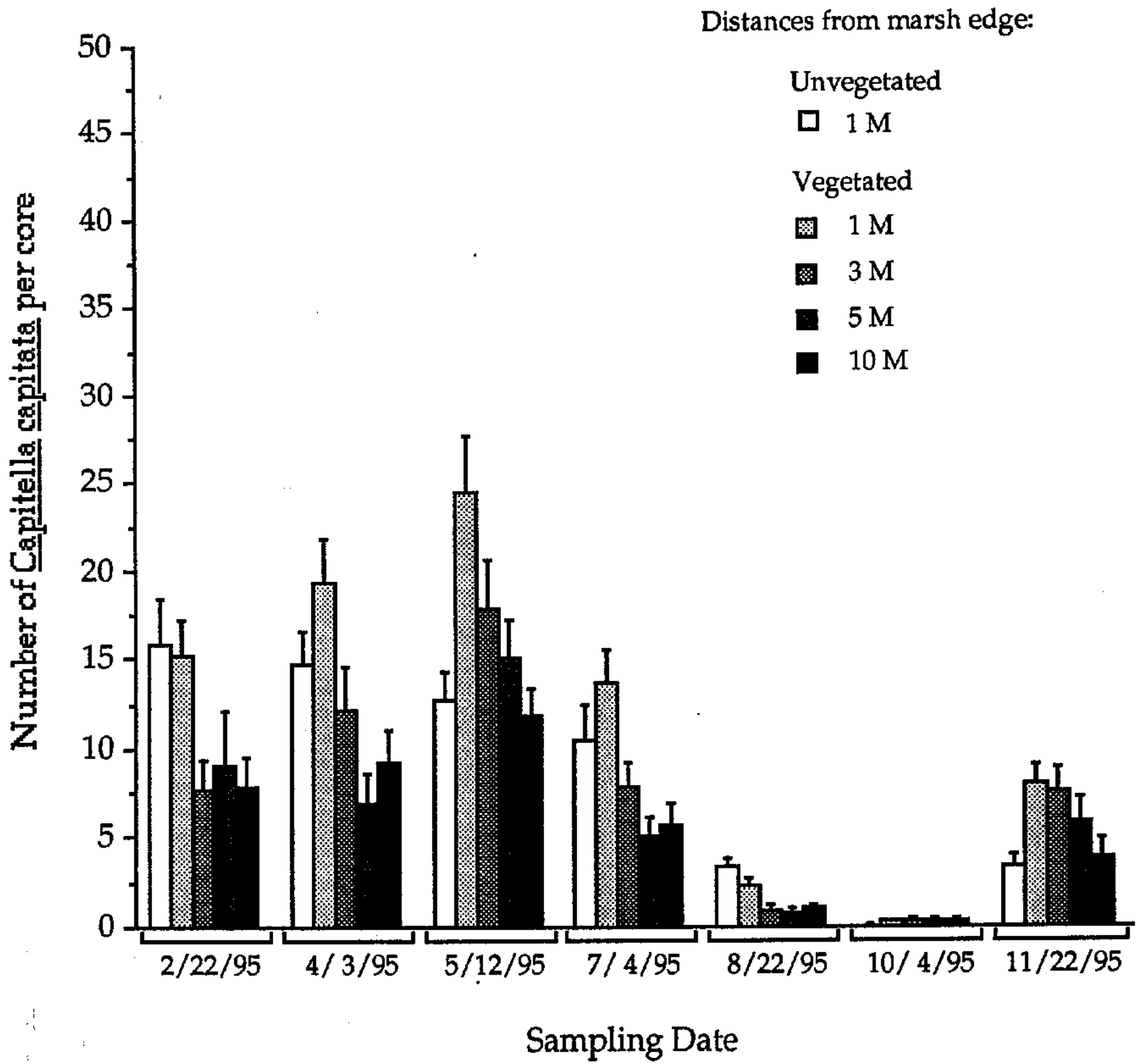
Figure 4.   Mean densities of Capitella capitata in the five microhabitats for each sampling date. Each mean represents data from 25 sediment cores; error bars indicate one standard error.   Each core had a surface area of 19.6 cm² and a depth of 5 cm.
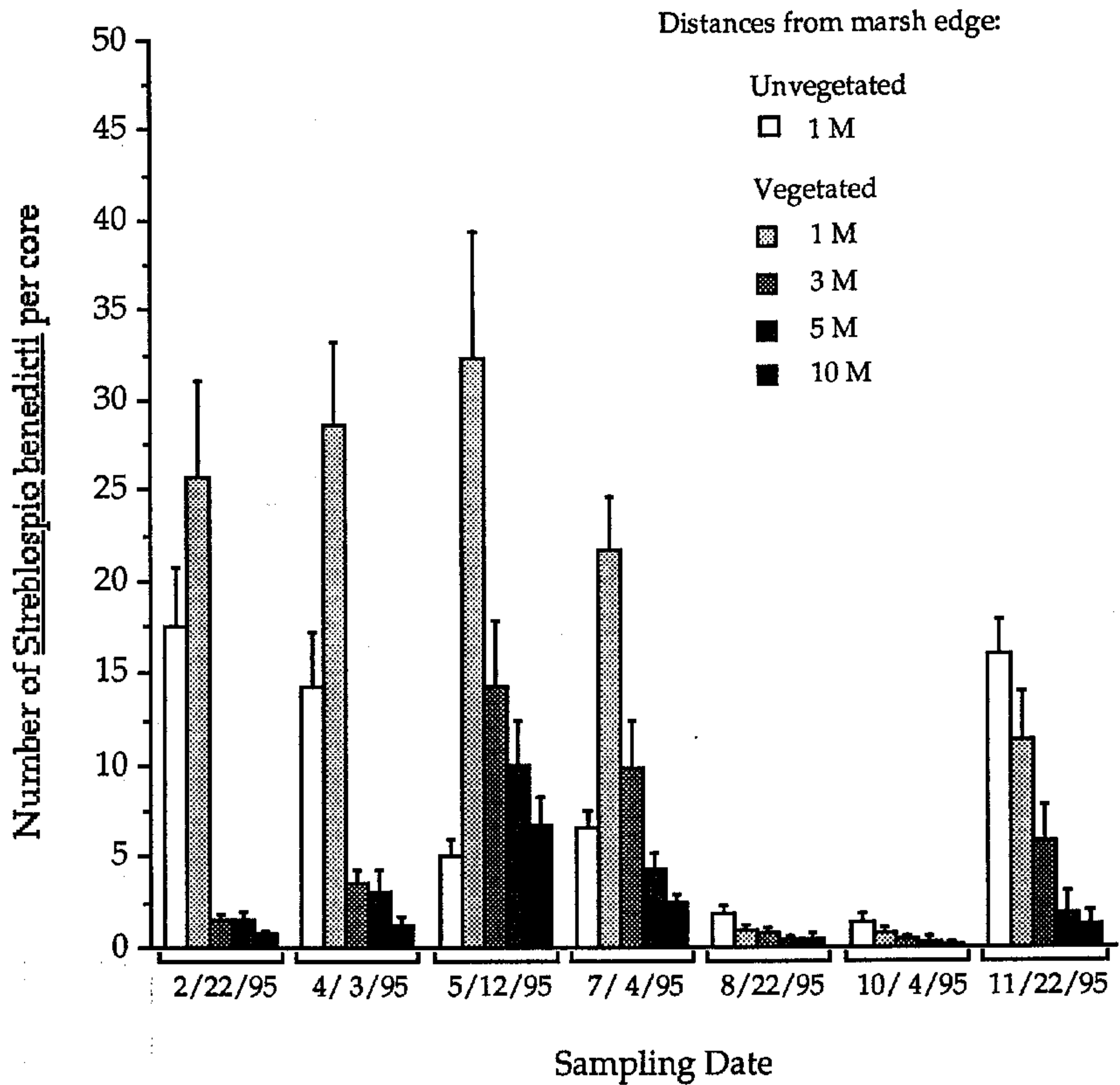
Figure 5.   Mean densities of Streblospio benedicti in the five microhabitats for each sampling date. Each mean represents data from 25 sediment cores; error bars indicate one standard error. Each core had a surface area of 19.6 cm² and a depth of 5 cm.
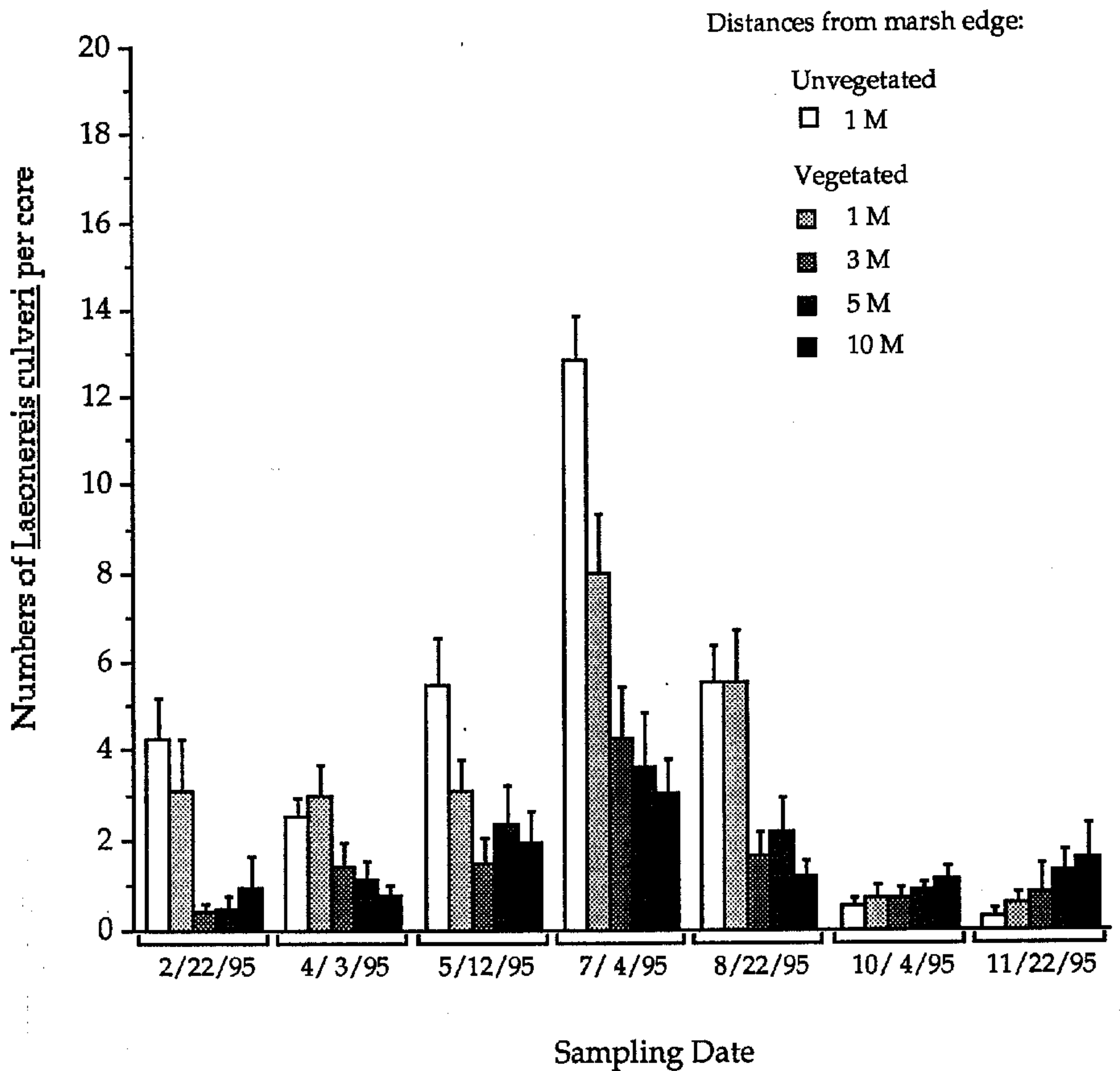
Figure 6.   Mean densities of <u>Laeonereis</u> <u>culveri</u> in the five microhabitats for each sampling date. Each mean represents data from 25 sediment cores; error bars indicate one standard error. Each core had a surface area of 19.6 cm^2 and a depth of 5 cm.
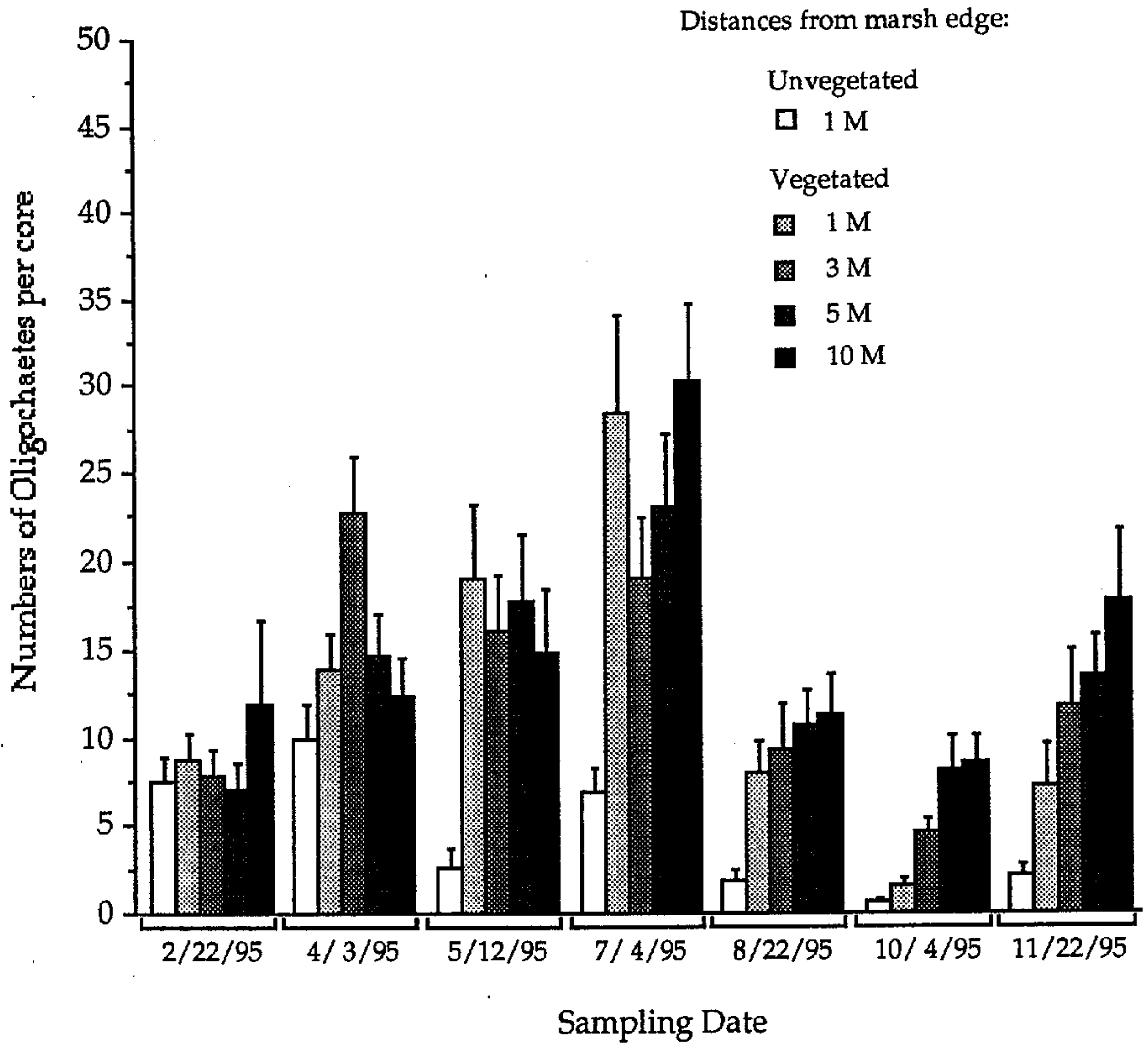
Figure 7.   Mean densities of oligochaetes in the five microhabitats for each sampling date. Each mean represents data from 25 sediment cores; error bars indicate one standard error. Each core had a surface area of 19.6 cm² and a depth of 5 cm.
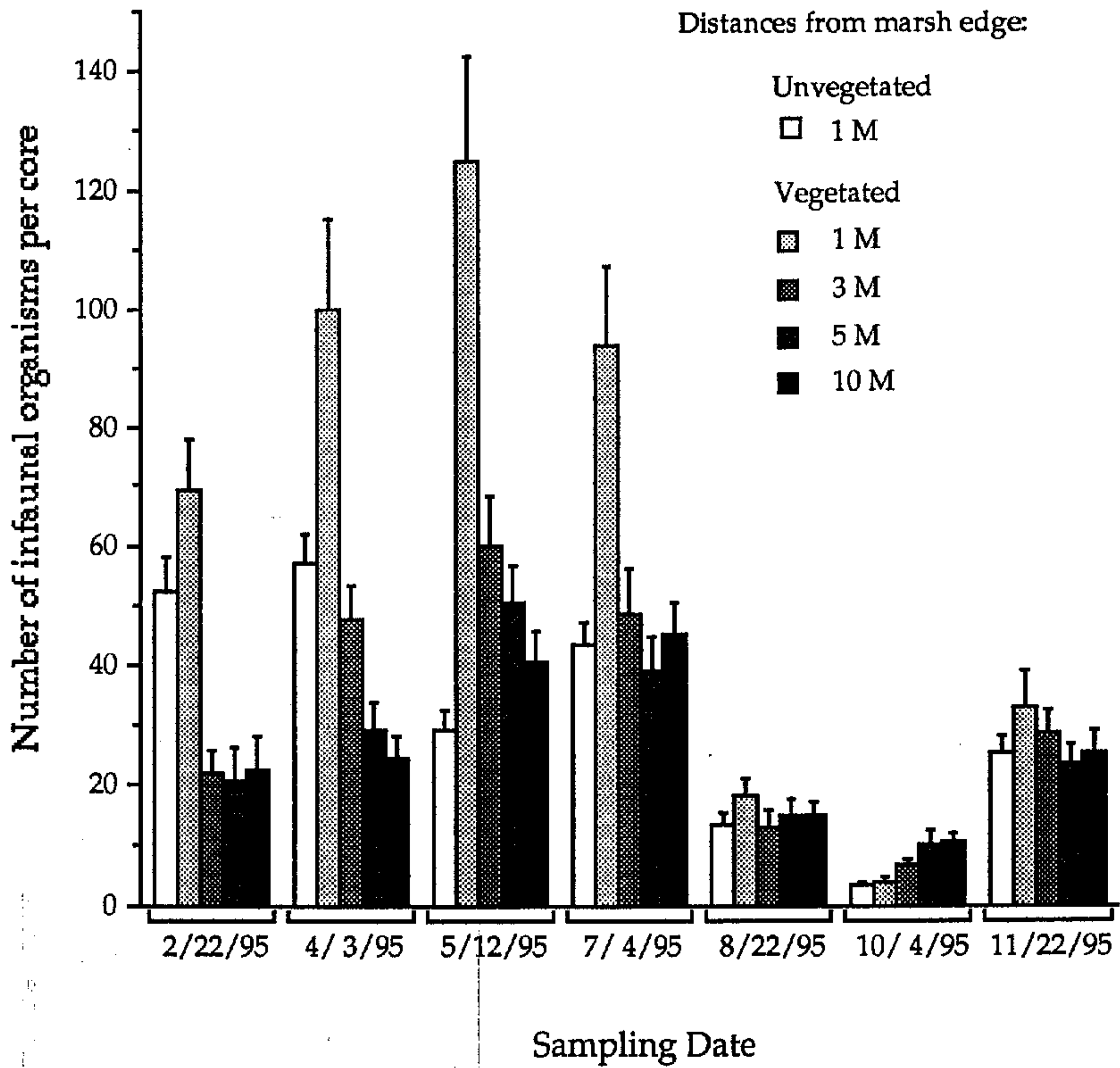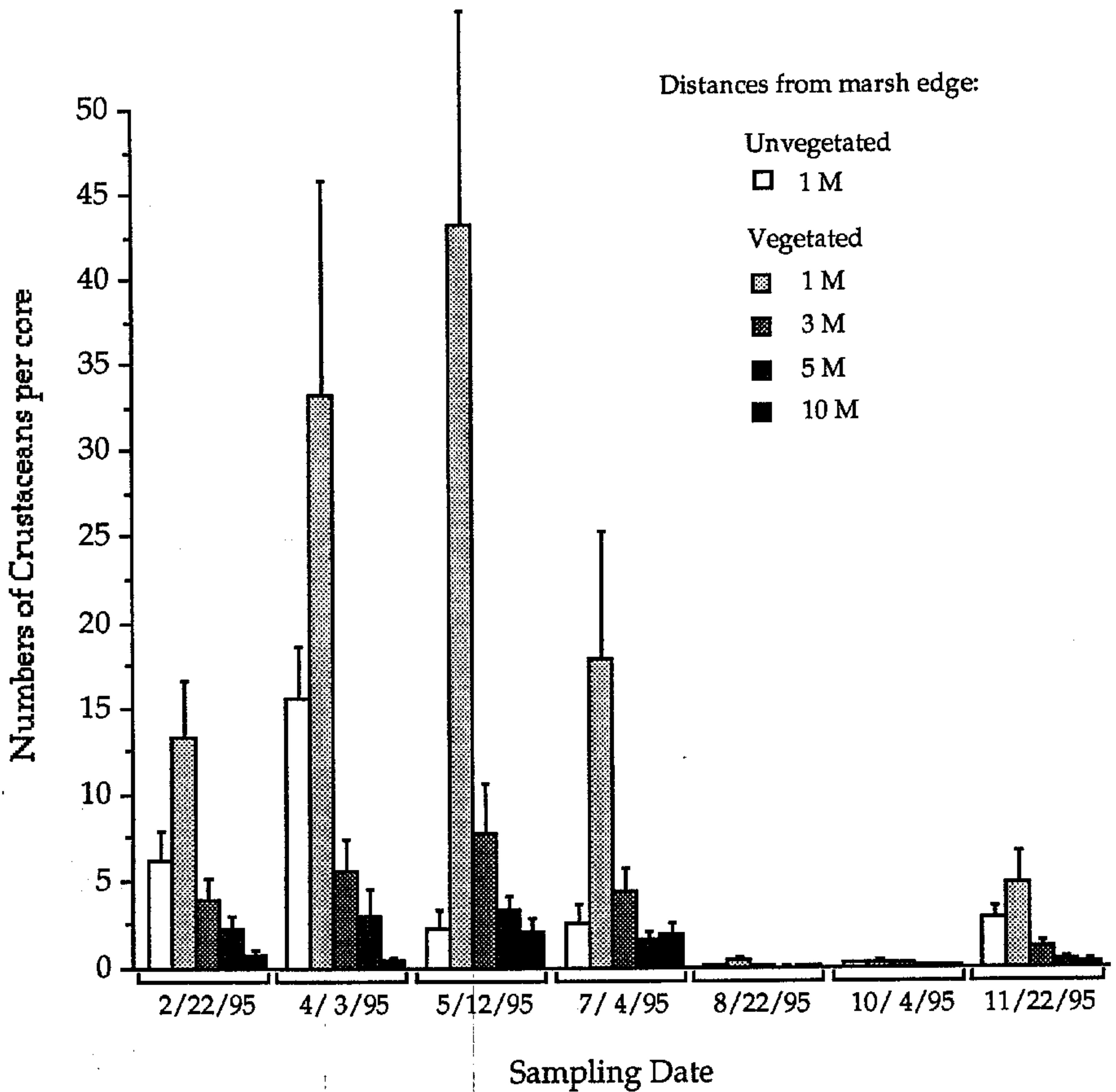
Figure 8.   Mean densities of crustaceans among the five microhabitats for each sampling date. Each mean represents data from 25 sediment cores; error bars indicate one standard error. Each core had a surface area of 19.6 cm² and a depth of 5 cm.

Table 2. Results from one-way ANOVA's comparing infaunal density and biomass among five microhabitats (Edge effect). Degrees of freedom are total (124), main effect of Edge (4), and residual error (120). P-values are listed for the main effect and each of four contrasts. Data for each month were analyzed independently. An asterisk denotes significance at an adjusted alpha level of 0.05 using the Sequential Bonferroni technique (Rice, 1988) to account for multiple tests (calculated for main effect only).

February	Main Effect of Edge		Contrasts			
			-1 M vs.	1 M vs.	-1 M vs.	-1 M vs.
Dependent Variable:	SS	P-value	1 M	3,5,10 M	1,3,5,10 M	10 M
Total Infauna	43.067	0.0001*	0.2836	0.0001	0.0002	0.0001
Polychaetes	84.399	0.0001*	0.4368	0.0001	0.0001	0.0001
Capitella capitata	31.065	0.0001*	0.5765	0.0001	0.0083	0.0046
Streblospio benedicti	106.987	0.0001*	0.2643	0.0001	0.0001	0.0001
Laeonereis culveri	21.592	0.0001*	0.0284	0.0025	0.0001	0.0001
Oligochaetes	2.261	0.6946	0.4583	0.5151	0.6640	0.4373
Crustaceans	37.814	0.0001*	0.0440	0.0001	0.0969	0.0009
Annelid biomass (mg)	38.736	0.0001*	0.3506	0.0001	0.0001	0.0001
Crustacean biomass (mg)	2.934	0.0013*	0.4317	0.0004	0.0715	0.0025

April	Main Effect of Edge		Contrasts			
			-1 M vs.	1 M vs.	-1 M vs.	-1 M vs.
Dependent Variable:	SS	P-value	1 M	3,5,10 M	1,3,5,10 M	10 M
Total Infauna	38.807	0.0001*	0.0238	0.0001	0.0037	0.0001
Polychaetes	72.823	0.0001*	0.1510	0.0001	0.0004	0.0001
Capitella capitata	32.691	0.0001*	0.2969	0.0001	0.0247	0.0064
Streblospio benedicti	114.847	0.0001*	0.0168	0.0001	0.0001	0.0001
Laeonereis culveri	11.679	0.0002*	0.9152	0.0001	0.0042	0.0011
Oligochaetes	14.015	0.0007*	0.0145	0.4778	0.0003	0.0509
Crustaceans	123.149	0.0001*	0.3229	0.0001	0.0001	0.0001
Annelid biomass (mg)	37.947	0.0001*	0.1422	0.0001	0.0001	0.0001
Crustacean biomass (mg)	17.008	0.0001*	0.5907	0.0001	0.0001	0.0001

May	Main Effect of Edge		Contrasts			
			-1 M vs.	1 M vs.	-1 M vs.	-1 M vs.
Dependent Variable:	SS	P-value	1 M	3,5,10 M	1,3,5,10 M	10 M
Total Infauna	25.759	0.0001*	0.0001	0.0001	0.0001	0.1858
Polychaetes	16.881	0.0001*	0.0004	0.0001	0.3069	0.2618
Capitella capitata	8.149	0.0146*	0.0097	0.0015	0.4247	0.4702
Streblospio benedicti	43.371	0.0001*	0.0001	0.0001	0.0023	0.6026
Laeonereis culveri	14.264	0.0001*	0.0826	0.0687	0.0004	0.0022
Oligochaetes	54.923	0.0001*	0.0001	0.8860	0.0001	0.0001
Crustaceans	78.185	0.0001*	0.0001	0.0001	0.0005	0.9366
Annelid biomass (mg)	6.521	0.0040*	0.9393	0.0023	0.0223	0.0025
Crustacean biomass (mg)	6.613	0.0001*	0.0001	0.0001	0.0029	0.6680

July	Main Effect of Edge		Contrasts			
			-1 M vs.	1 M vs.	-1 M vs.	-1 M vs.
Dependent Variable:	SS	P-value	1 M	3,5,10 M	1,3,5,10 M	10 M
Total Infauna	13.210	0.0001*	0.0014	0.0001	0.7841	0.6423
Polychaetes	44.186	0.0001*	0.3422	0.0001	0.0002	0.0001
Capitella capitata	18.762	0.0001*	0.1439	0.0001	0.1240	0.0256
Streblospio benedicti	51.186	0.0001*	0.0001	0.0001	0.6963	0.0028
Laeonereis culveri	45.789	0.0001*	0.0053	0.0001	0.0001	0.0001
Oligochaetes	32.174	0.0001*	0.0001	0.9263	0.0001	0.0001
Crustaceans	23.059	0.0001*	0.0002	0.0001	0.1366	0.7970
Annelid biomass (mg)	15.795	0.0002*	0.9332	0.0003	0.0033	0.0016
Crustacean biomass (mg)	0.625	0.4564	0.4174	0.0968	0.7899	0.2900

Table 2. continued

August	Main Effect of Edge		Contrasts			
			-1 M vs. 1 M	1 M vs. 3,5,10 M	-1 M vs. 1,3,5,10 M	-1 M vs. 10 M
Dependent Variable:	SS	P-value				
Total Infauna	1.304	0.8127	0.8502	0.6232	0.5358	0.6111
Polychaetes	30.909	0.0001*	0.0793	0.0002	0.0001	0.0001
Capitella capitata	11.689	0.0001*	0.0615	0.0064	0.0001	0.0001
Streblospio benedicti	6.471	0.0009*	0.0184	0.1426	0.0001	0.0004
Laeonereis culveri	26.346	0.0001*	0.2306	0.0001	0.0001	0.0001
Oligochaetes	30.467	0.0001*	0.0039	0.1604	0.0001	0.0001
Crustaceans	0.7308	0.0357	0.0332	0.0020	0.7822	1.0000
Annelid biomass (mg)	30.971	0.0001*	0.0026	0.0001	0.0001	0.0001
Crustacean biomass (mg)	0.006	0.8533	0.4030	0.8920	0.3409	0.5881

October	Main Effect of Edge		Contrasts			
			-1 M vs. 1 M	1 M vs. 3,5,10 M	-1 M vs. 1,3,5,10 M	-1 M vs. 10 M
Dependent Variable:	SS	P-value				
Total Infauna	21.465	0.0001*	0.8762	0.0001	0.0033	0.0001
Polychaetes	0.739	0.8417	0.3805	0.9999	0.2677	0.2832
Capitella capitata	0.596	0.2376	0.2316	0.5016	0.0432	0.0958
Streblospio benedicti	4.4	0.0037*	0.0863	0.0855	0.0006	0.0004
Laeonereis culveri	1.096	0.4427	0.9299	0.2355	0.3027	0.1760
Oligochaetes	42.518	0.0001*	0.3347	0.0001	0.0001	0.0001
Crustaceans	0.297	0.4891	0.7389	0.2534	0.6418	0.3183
Annelid biomass (mg)	0.047	0.9476	0.9503	0.5689	0.6029	0.6460
Crustacean biomass (mg)	0.142	0.2809	0.8872	0.6487	0.5946	0.9355

November	Main Effect of Edge		Contrasts			
			-1 M vs. 1 M	1 M vs. 3,5,10 M	-1 M vs. 1,3,5,10 M	-1 M vs. 10 M
Dependent Variable:	SS	P-value				
Total Infauna	2.211	0.4127	0.4840	0.1486	0.8121	0.5800
Polychaetes	42.575	0.0001*	0.9202	0.0001	0.0001	0.0001
Capitella capitata	14.684	0.0003*	0.0003	0.0046	0.0152	0.8700
Streblospio benedicti	95.162	0.0001*	0.0124	0.0001	0.0001	0.0001
Laeonereis culveri	2.456	0.1804	0.6176	0.3248	0.1644	0.0702
Oligochaetes	42.813	0.0001*	0.0638	0.0008	0.0001	0.0001
Crustaceans	19.3967	0.0001*	0.6591	0.0001	0.0013	0.0001
Annelid biomass (mg)	5.077	0.0272	0.1249	0.0155	0.9589	0.0962
Crustacean biomass (mg)	0.863	0.0016*	0.0537	0.0001	0.5152	0.0775

nonvegetated densities declined earlier than marsh edge densities and were significantly lower than edge densities by the April 3rd sampling period. As numbers of infauna in all microhabitats increased in the late fall (November sampling period), mean densities of total infauna were again highest at the marsh edge (Figure 2).

The seasonal pattern for polychaetes in general, Capitella capitata, Streblospio benedicti, and crustaceans was similar to that of total infauna (Figures 3 - 5, 8). However, the ratio of individuals on the marsh edge compared to densities in other microhabitats varied in magnitude among taxonomic groups. Streblospio benedicti and crustaceans had the highest proportion of individuals found on the marsh edge; mean densities in this microhabitat often reached levels more than twice as high as those in any other microhabitat. The greatest difference among microhabitats occurred in May when densities of crustaceans on the marsh edge were more than five times higher than those in any other microhabitat. Although abundances of overall polychaetes and Capitella capitata were also highest on the marsh edge for most of the year, differences among microhabitats were not as large as differences for Streblospio benedicti and crustaceans.

Seasonal patterns for annelid and crustacean biomass were generally similar to abundance patterns; marsh edge habitats had the highest biomass within vegetated microhabitats (Figures 9 and 10, Table 2). In April and May, however, the highest annelid biomass occurred in nonvegetated microhabitats while annelid abundance was highest in vegetation. This difference occurred because Laeonereis culveri, a large omnivorous polychaete, was most abundant in the nonvegetated microhabitat (Figure 6).
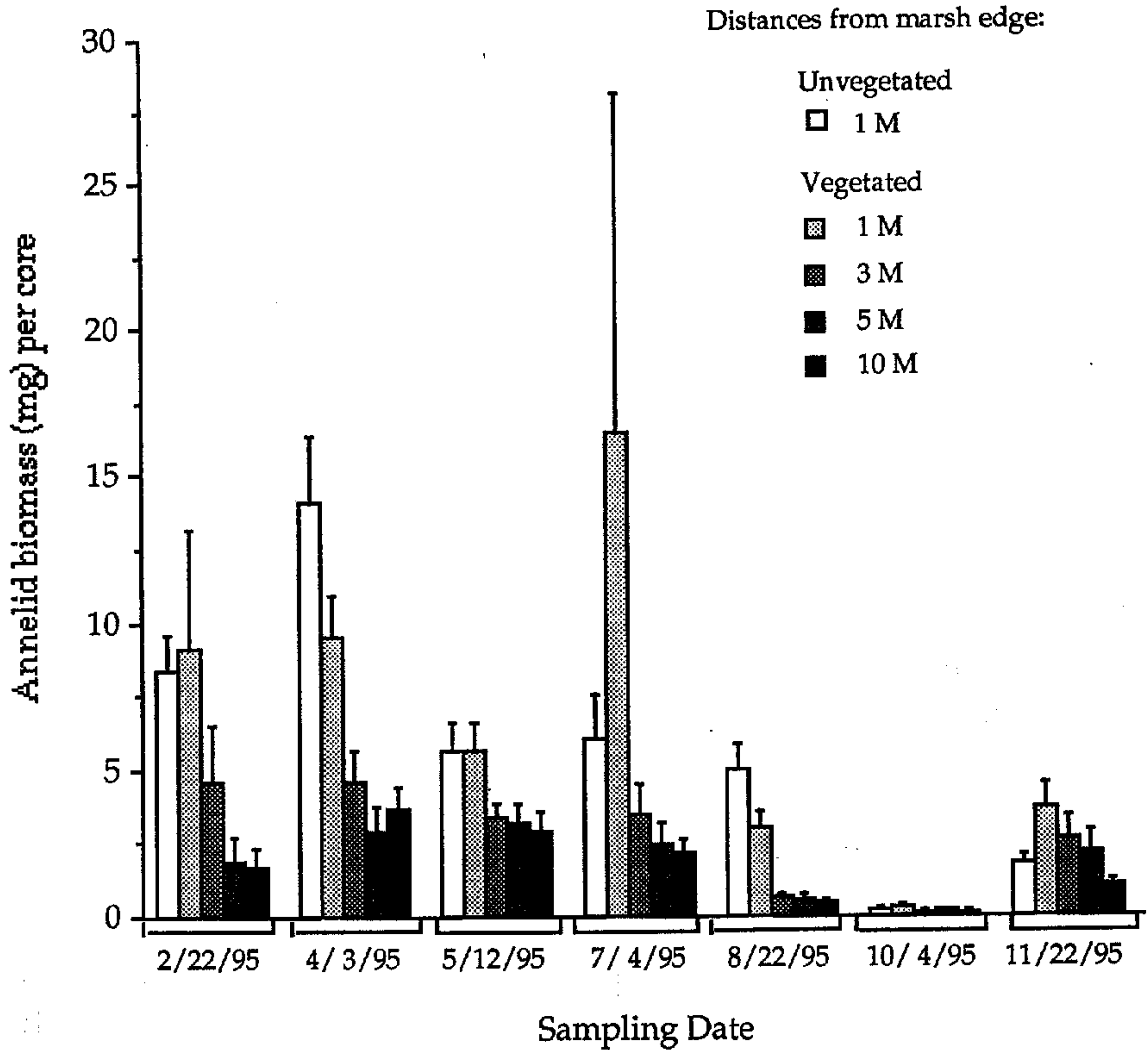
Figure 9.   Mean annelid biomass (mg) in the five microhabitats for each sampling date. Each mean represents data from 25 sediment cores; error bars indicate one standard error. Each core had a surface area of 19.6 cm² and a depth of 5 cm.
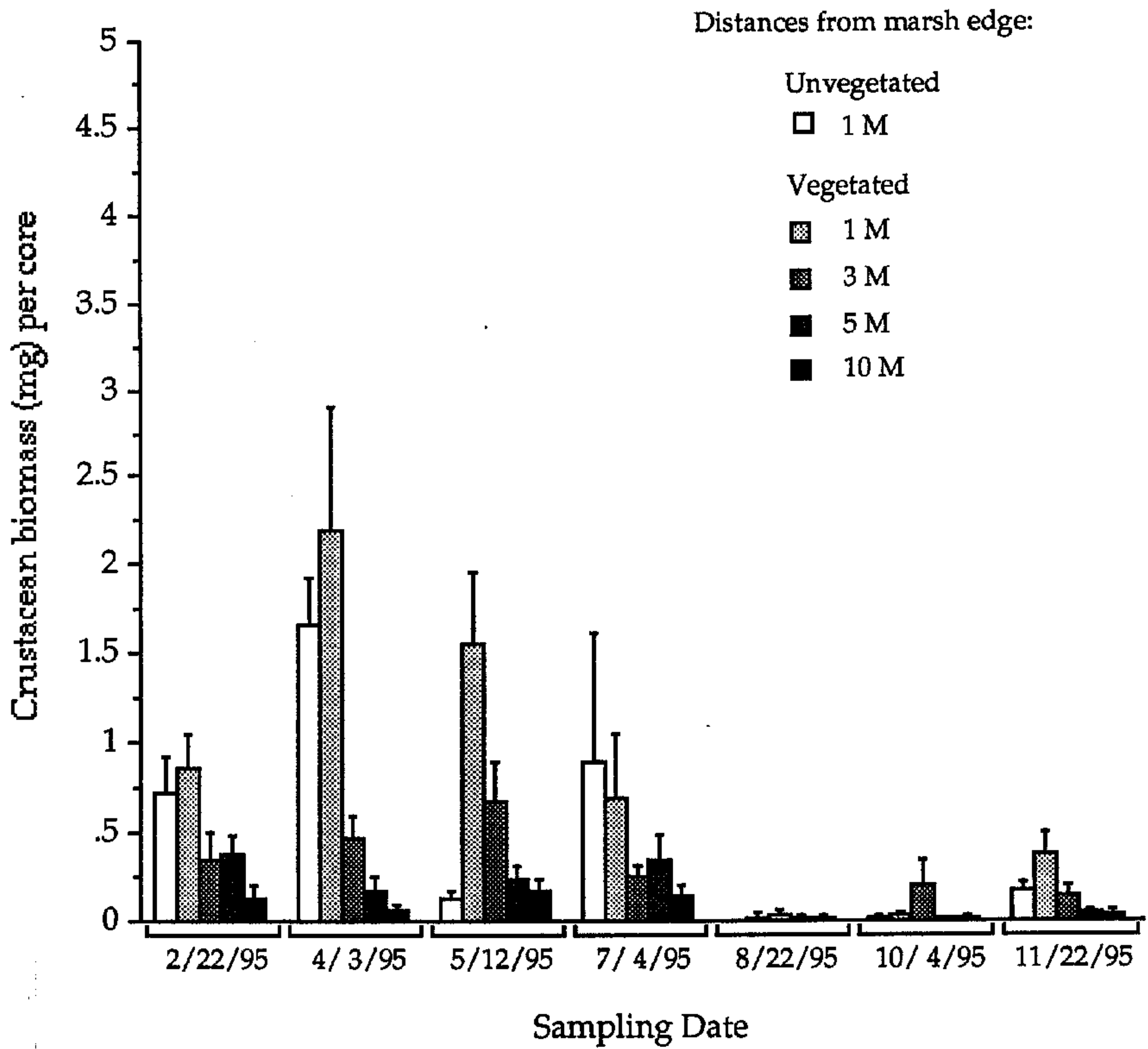
Figure 10.   Mean crustacean biomass (mg) in the five microhabitats for each sampling date. Each mean represents data from 25 sediment cores; error bars indicate one standard error. Each core had a surface area of 19.6 cm² and a depth of 5 cm.

In contrast to most infaunal abundance and biomass data, oligochaete abundances were similar among marsh microhabitats. Mean oligochaete densities were frequently highest in microhabitats farthest (10M) from the marsh edge (Figure 7). Although oligochaetes showed no affinity for marsh edge habitat, densities were consistently higher on the vegetated marsh surface than in nonvegetated microhabitats.

Edge and Elevation Effects on Infauna Distribution

Within the four vegetated microhabitats, the importance of distance to the edge in relation to elevation varied among the sampling periods. There was a significant negative linear relationship between elevation and infaunal abundance during four of the seven sampling periods (Table 3). The multivariate analyses, however, detected a constant and highly significant edge effect for overall infauna throughout the year after adjusting for elevation effects when necessary (Table 3).

Abundances of overall polychaetes, Streblospio benedicti, and overall crustaceans were related to distance to the edge throughout the year except in February and October when densities of individual taxonomic groups were low throughout the marsh (Table 3, univariate results). However, Laeonereis culveri, and oligochaetes were generally not affected by distance to the edge (Table 3, Figures 11 and 12).

Densities of polychaetes, Capitella capitata, Laeonereis culveri, and annelid biomass were related to elevation in the spring and mid-summer. Streblospio benedicti abundances were only related to elevation in the summer (July - significant interactions, p = 0.0338 and August). Abundances of oligochaetes and crustaceans were related to elevation in the spring and

Table 3. Results from MANOVA and MANCOVA testing for edge and elevation effects on infaunal abundance (only data from the marsh surface were used in this analysis). Multivariate F-statistics correspond to Wilks' lambda statistic. I used MANCOVA when elevation, the covariate, was a significant factor in preliminary tests and slopes of the abundance - elevation or the biomass-elevation relationship were homogenous (February and July). If elevation was not significant (p > 0.05), I applied MANOVA to test for edge effects (May, August, and October). Five of the seven sampling periods were analyzed using these methods. Because edge*elevation interactions were significant (slopes were not homogeneous) for multivariate tests in April and November, neither MANCOVA nor MANOVA models would adequately describe the relationships between these factors and dependent variables. Occasionally, factor interactions were significant for dependent variables within the univariate analyses; these are denoted by a "-". All animal abundance and biomass data were log-transformed, $Ln(y + 1)$.

	Multivariate								Univariate										
							Capitella		Streblospio		Laeonereis						Annelid		Crustacean
	df	F	P	df	Polychaetes	df	capitata	df	benedicti	df	culveri	df	Oligochaetes	df	Crustaceans	df	Wt (mg)	df	Wt (mg)
Source:																			
February																			
Edge	24, 255.8	1.703	0.0241	3	0.4587	3	0.9568	3	0.0001	3	0.8266	3	0.572		-	3	0.8685	3	0.3446
Elevation	8, 88	4.075	0.0005	1	0.0002	1	0.0009			1	0.0038				-	1	0.0001	1	0.0220
April																			
Edge	24, 247.1	2.399	0.0004	3	0.0427	3	0.0082	3	0.0001	3	0.1702	3	0.0005	3	0.0587	3	0.0958	3	0.2173
Elevation	8, 85	11.62	0.0001	1	0.0001	1	0.0001			1	0.0062	1	0.0034	1	0.0475	1	0.0001	1	0.2228
Edge*Elevation	24, 247.1	2.408	0.0004	3	0.0043	3	0.0025					3	0.0006	3	0.0013	3	0.0483	3	0.0451
May																			
Edge	24, 258.7	2.707	0.0001	3	0.0002	3	0.0136	3	0.0001	3	0.2249	3	0.9409		-	3	0.0126	3	0.0001
Elevation															-				
July																			
Edge	24, 255.8	2.368	0.0005	3	0.0073	3	0.1927		-	3	0.9142	3	0.2687	3	0.0002	3	0.4977	3	0.1676
Elevation	8, 88	5.289	0.0001	1	0.0001	1	0.0004		-	1	0.0001					1	0.0042		
August																			
Edge	24, 258.7	2.795	0.0001	3	0.0024	3	0.0504	3	0.0086	3	0.0009	3	0.4034	3	0.0226	3	0.0001	3	0.9514
Elevation								1	0.0024										
October																			
Edge	24, 258.7	2.001	0.0046	3	0.9812	3	0.7559	3	0.163	3	0.4781	3	0.0561	3	0.3161	3	0.9233	3	0.2667
Elevation												1	0.0002						
November																			
Edge	24, 255.8	2.253	0.0009	3	0.0224	3	0.004	3	0.0001	3	0.2892	3	0.0518	3	0.0455	3	0.0213		0.0010
Elevation	8, 88	3.1630	0.0035	1	0.9725	1	0.0664					1	0.0082	1	0.0001				0.3310
Edge*Elevation	24, 247.1	2.224	0.0012	3	0.0430							3	0.0414						0.0018

Polychaetes
Ln(density+1)

Distance to Marsh Edge (M)

Capitella capitata
Ln(density+1)

Distance to Marsh Edge (M)

Laeonereis culveri
Ln(density+1)

Distance to Marsh Edge (M)

Annelid Biomass
Ln(mg+1)

Distance to Marsh Edge (M)

Crustacean Biomass
Ln(mg+1)

Distance to Marsh Edge (M)
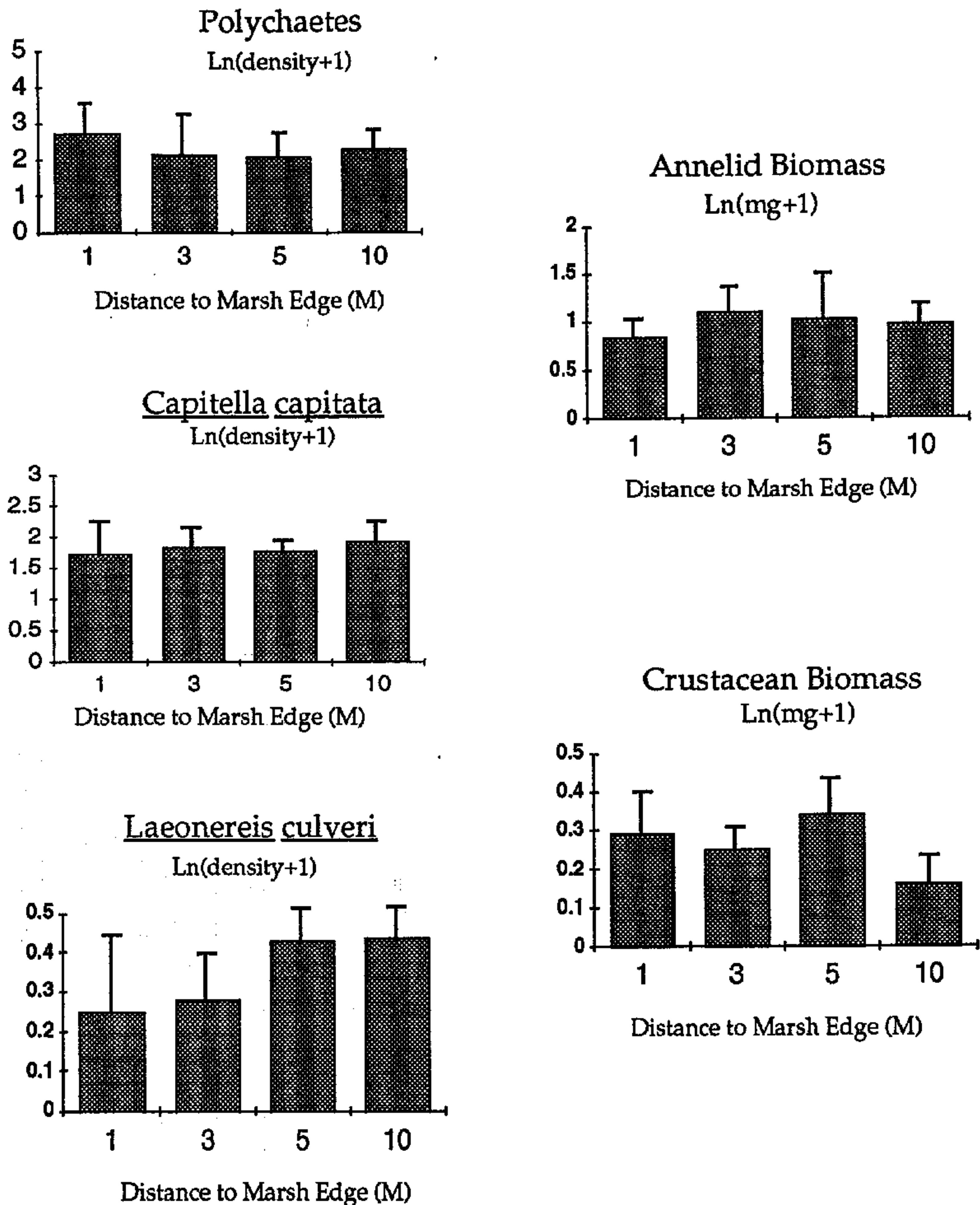
Figure 11.   The least square means for each vegetated microhabitat in February; means represent the edge effect after removing elevation effect. Error bars indicate one standard error. All abundance and biomass data were transformed using the Ln(y+1) transformation. Each graph has a different scale on the Y-axis.

Polychaetes
Ln(density+1)

Distance to Marsh Edge (M)

Capitella capitata
Ln(density+1)

Distance to Marsh Edge (M)

Laeonereis culveri
Ln(density+1)

Distance to Marsh Edge (M)

Annelid Biomass
Ln(mg+1)

Distance to Marsh Edge (M)
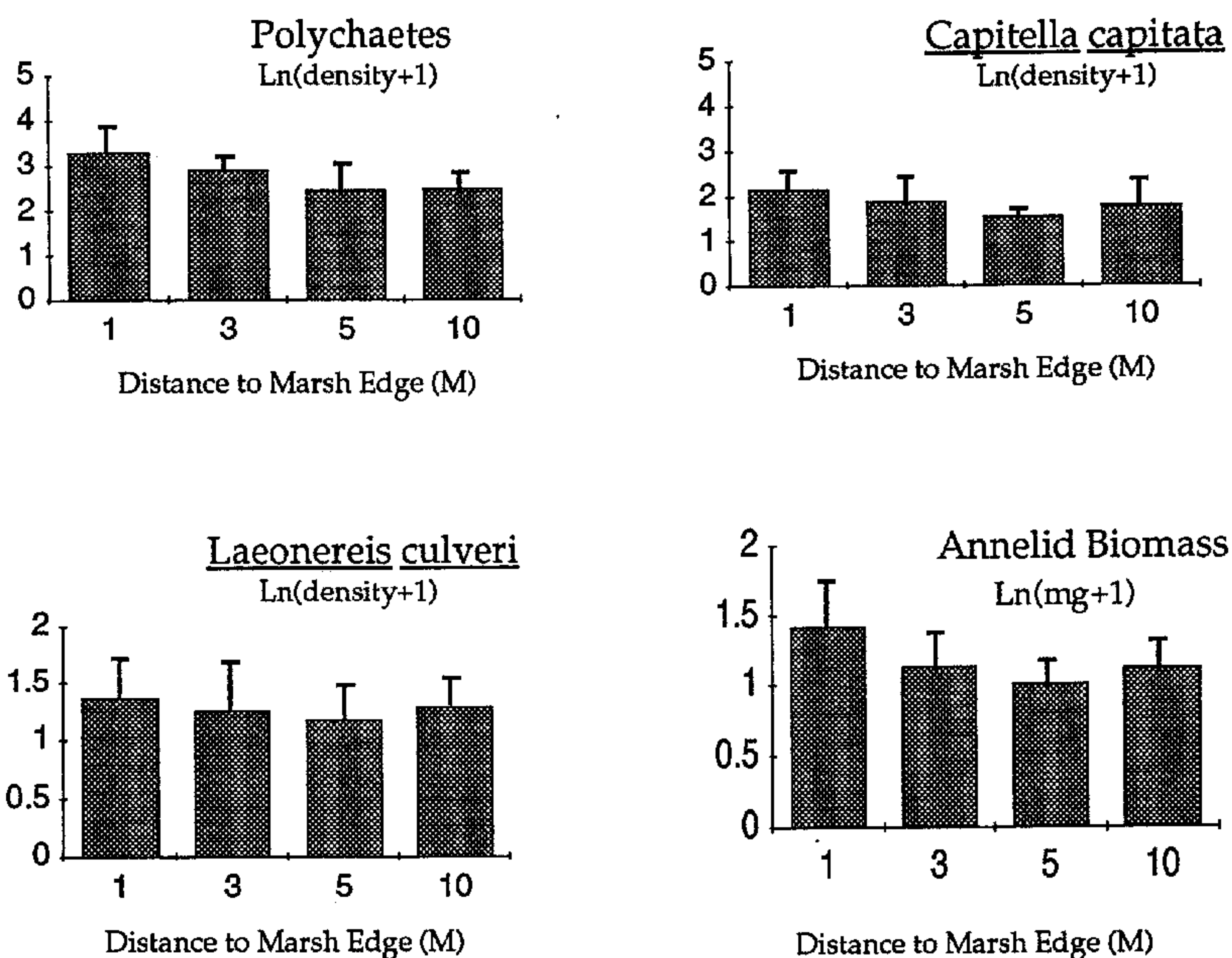
Figure 12.   The least square means for each vegetated microhabitat in July; means represent the edge effect after removing elevation effect. Error bars indicate one standard error. All abundance and biomass data were transformed using the Ln(y+1) transformation. Each graph has a different scale on the Y-axis.

fall. When densities were low during October, only densities of oligochaetes were related to elevation.

Physical/Chemical Factors and Sediment Characteristics

Water temperature ranged from a low of 5 ºC in December to a high of 39 ºC in July (Figure 13). Sediment temperature varied among microhabitats, and daily fluctuation generally increased with increasing elevation and decreasing water depth (Figure 14). Therefore, the most stable temperatures usually occurred in nonvegetated habitats, whereas the widest temperature fluctuations occurred ten meters from the marsh edge. In May through July, however, sediment temperatures in the nonvegetated microhabitat were often similar or higher than temperatures at the marsh edge. Vegetation may have shaded sediments within the marsh during the summer.

Water levels were lowest in the winter and early spring, especially after the passage of cold fronts (Figure 13). Water levels peaked in spring and early fall. From March to June, water levels were high but variable. From near the end of July through the beginning of October, water levels were consistently high due to the presence of Tropical Storm Dean and Hurricane Opal in the Gulf of Mexico. These water level patterns caused inundation patterns of microhabitats to be seasonally variable (Table 4). In January/February, for example, marsh microhabitats were inundated less than three percent of the time and the nonvegetated microhabitat was only inundated 26% of the time. In contrast, during August/October, all microhabitats were inundated for over 99% of the time. Water salinity ranged from a low of 9.8 ppt in April to a high of 28.2 ppt in September and
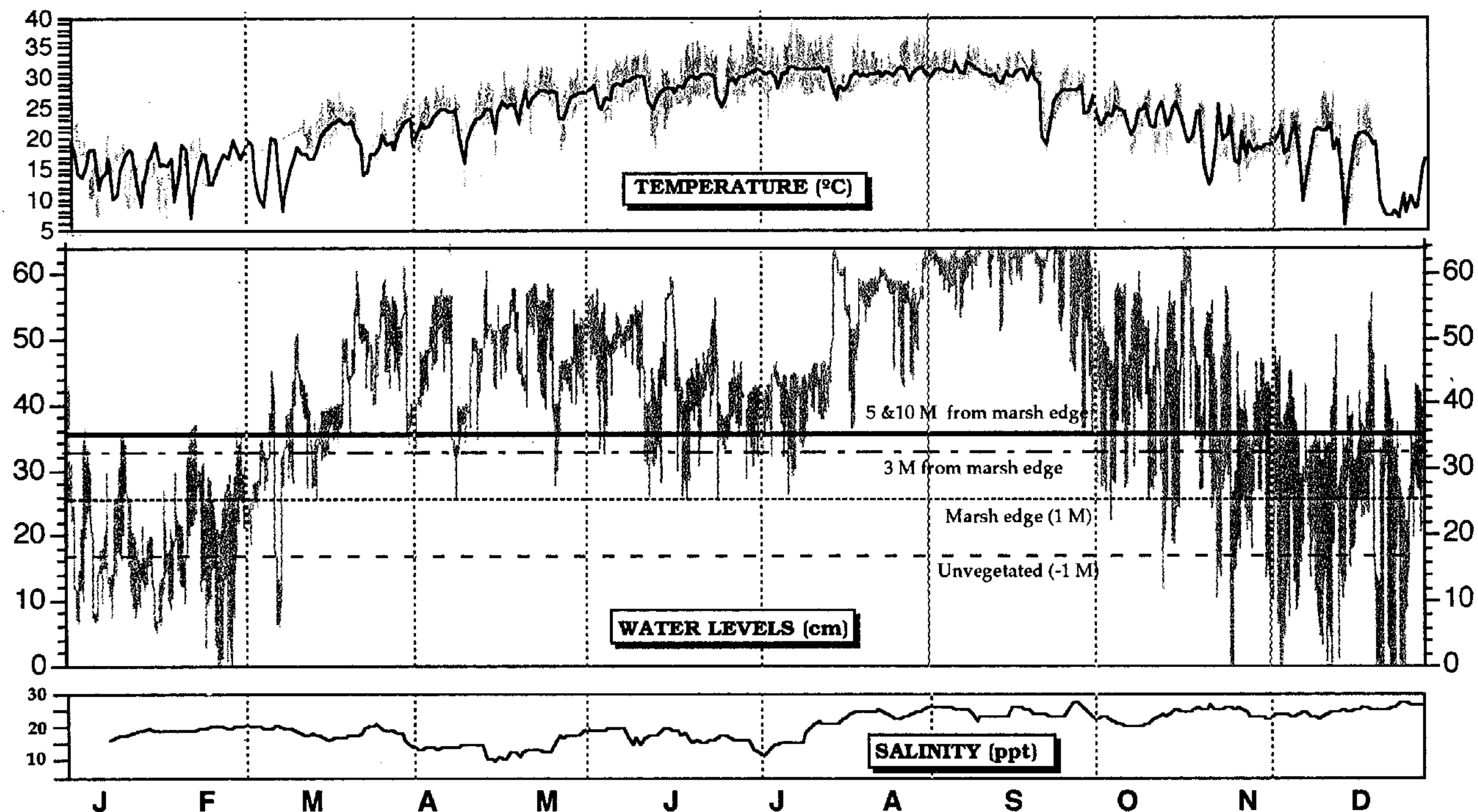
Figure 13.   Temperature, water level, and salinity measured at Gang's Bayou from January 11 to December 31, 1995. Starting from October 4 through December 31, water levels at the sample site were extrapolated from levels measured at NOAA tide station #887-1450 in the Galveston Ship Channel (29° 18.6′ N and 94° 47.6′ W). Dotted vertical lines indicate sampling periods. Hourly water temperature (grey line) was plotted with daily mean air temperatures (black line). In the middle graph, dark grey lines represent hourly water levels. Hortizontal lines are mean relative elevations for each of the five transects sampled. Daily mean salinities for 1995 were calculated from hourly data.

Sediment Temperatures (°C)
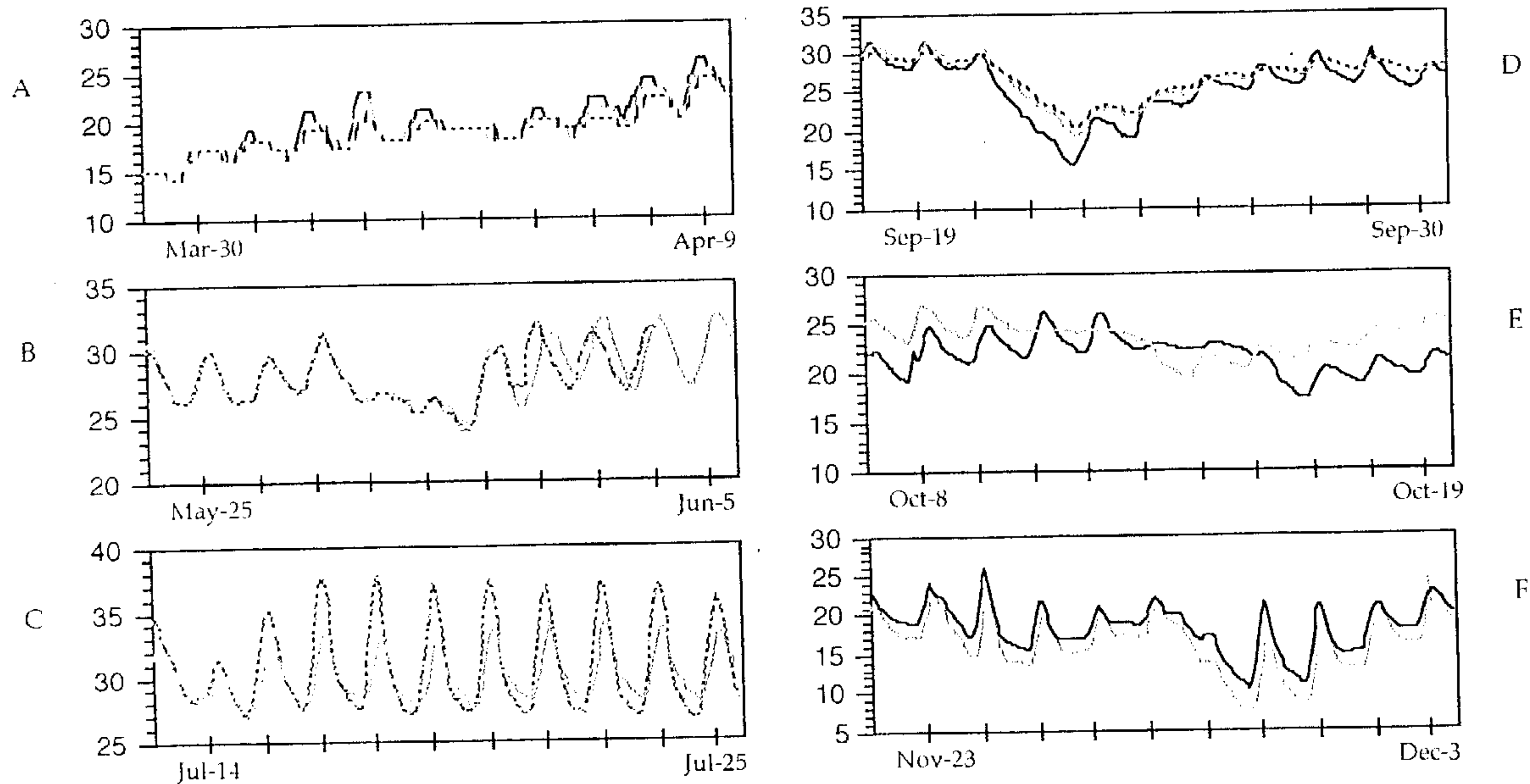
Figure 14.   Typical daily sediment temperature fluctuations for three microhabitats within the intertidal salt marsh at Gang's Bayou: unvegetated (1 M downslope of marsh edge) = dotted line, marsh edge (1 M) = grey line, and 10 M away from the nearest edge (10 M) = black line. Tick marks indicate 12:00 noon. The ranges of temperature fluctuation (y-axes) are different for each graph. A continuous data set at each microhabitat for 1995 was not obtained.

Table 4. The daily average percent of time that microhabitats were inundated for each six-week period.

Distance from the Marsh Edge	-1 M		1 M		3 M		5 M		10 M	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Jan 11 - Feb 21, 1995	26%	0.83%	3%	0.28%	0%	0.01%	0%	0.01%	0%	0.02%
Feb 22-April 3, 1995	74%	1.17%	45%	1.42%	28%	1.26%	20%	1.11%	24%	1.21%
April 4 - May 11, 1995	100%	0.11%	87%	0.90%	70%	1.20%	61%	1.22%	67%	1.22%
May 12 - July 3, 1995	98%	0.22%	82%	0.93%	64%	1.21%	58%	1.24%	56%	1.27%
July 4 - Aug 21, 1995	100%	0.05%	89%	0.76%	63%	1.37%	54%	1.43%	55%	1.43%
Aug 22 - Oct 3, 1995	100%	0.01%	100%	0.08%	99%	0.13%	99%	0.14%	99%	0.14%
Oct 4 - Nov 21, 1995	85%	0.68%	60%	0.98%	43%	1.02%	39%	0.98%	36%	0.95%

December. Sharp drops in salinity in the late spring and summer corresponded to the occurrence of local rainstorms. Salinity gradually increased through the fall and winter.

The amount of organic matter in the sediment varied substantially among intertidal microhabitats. Sediment organic content (SOC) and the amount of below-ground living macroorganic matter (LMOM) generally increased as microhabitat elevation and distance from the marsh edge increased (Tables 5 and 6) with highest levels occurring in vegetated microhabitats located 10 M from the marsh edge. Although SOC was positively correlated with elevation, and negatively related to total infauna abundance (Table 7), LMOM was not correlated with either elevation or infauna abundance. In addition, the amount of detritus (dead macroorganic matter) was negatively correlated with elevation but was not signficantly related to edge or total infauna abundance.

Sediment grain size and the degree of sorting varied among intertidal microhabitats. Sediment grain size generally decreased as microhabitat elevation and distance from the marsh edge increased (Tables 5-7). The degree of sediment grain sorting also decreased as distance from the edge increased, with the nonvegetated microhabitat considered moderately-sorted and all vegetated microhabitats considered poorly-sorted (Folk 1980). Mean grain size (μm) was found to be positively correlated with total infauna abundance, and negatively related to elevation (Table 7).

Table 5.   Sediment characteristics at five microhabitats within the intertidal salt marsh in Gang's Bayou. Each mean and standard error (SE) was calculated from 25 cores taken along five transects at various distances from the marsh edge. Mean particle size is in micrometers. The sorting parameter is a measure of the spread in the particle size-frequency distribution; well-sorted sediments have smaller phi values. Mean particle size and sorting were calculated using the method of moments as described by Folk (1980). Sediment Organic Content is described as a mean percentage of the weight of the core sample. The amount of living and dead macroorganic matter is shown as grams of dry weight.

Distance from Marsh Edge:	% Sand Fraction			% Silt			Mean Grain Size (μm)	Sorting (Phi)	Sediment Organic Content (%)	Macroorganics			
			Very							Living (g)		Detritus (g)	
	Medium	Fine	Fine	Coarse	Fine	% Clay				Mean	SE	Mean	SE
-1 M (Unveg)	0.84%	28.33%	45.75%	10.67%	2.81%	11.60%	93	0.9612	1.58	0.006	0.00	0.9994	0.10
1 M	0.96%	20.23%	38.74%	13.44%	4.46%	22.16%	81	1.0812	2.17	1.2367	0.20	1.1008	0.10
3 M	1.27%	14.85%	30.09%	17.00%	5.84%	30.95%	78	1.2435	4.72	1.4202	0.16	1.2008	0.12
5 M	1.45%	11.43%	25.88%	18.88%	8.45%	33.92%	65	1.3988	4.60	1.5658	0.15	0.9185	0.06
10 M	1.22%	10.73%	22.57%	20.10%	10.37%	34.99%	51	1.4285	5.70	2.1141	0.15	0.8669	0.08

Table 6.   Results from one-way ANOVA's sediment characteristics among five microhabitats (Edge effect). Degrees of freedom are total (124), main effect of Edge (4), and residual error (120). P values are shown for the main effect and each of four contrasts. Macroorganic data were transformed using Ln(y+1). An asterisk indicates significance at an adjusted alpha level of 0.05 using the Sequential Bonferroni technique (Rice, 1988) to account for multiple tests (calculated for main effect only).

Sediment characteristic:	Main Effect of Proximity to Edge	Contrasts			
		-1 M vs. 1 M	1 M vs. 3,5,10 M	-1 M vs. 1,3,5,10 M	-1 M vs. 10 M
% Sand	0.0001*	0.0006	0.0001	0.0001	0.0001
Mean Grain Size	0.0001*	0.1189	0.0001	0.0001	0.0001
Sediment Organic Content	0.0001*	0.3061	0.0001	0.0001	0.0001
Living Macroorganic Matter	0.0001*	0.0001	0.0011	0.0001	0.0001
Dead Macroorganic Matter (detritus)	0.1088	-	-	-	-

Table 7.   Pearson product-moment correlations between sediment characterstics, elevation, and total infauna abundance in marsh habitats (excluding -1 M transect). Animal abundances and macroorganic data were log-transformed.

	Elevation		Total Infauna Abundance	
	r	p	r	p
% Sand	-0.5780	0.0001	0.3706	0.0001
Mean Grain Size	-0.4450	0.0001	0.2420	0.0175
Sediment Organic Content	0.4167	0.0001	-0.2867	0.0038
Macroorganic Matter: Living matter	0.2982	0.8151	0.0135	0.8940
Detritus (dead matter)	-0.2892	0.0035	0.1795	0.0739

Discussion

Infaunal distribution patterns in relation to marsh edge and elevation are important in understanding population dynamics within marsh systems. However, because distance to the marsh edge and elevation are generally confounded in marshes it is unknown whether elevation or edge effects are responsible for the observed patterns. The relative importance of these two marsh characteristics in relation to infaunal abundance suggests the dominance of different ecological mechanisms in the marsh (Table 8).

Elevation is often cited as the driving force behind the zonation of intertidal organisms; however, abundances of most surface-dwelling species (surface deposit feeders and suspension feeders) in this study were often more closely related to proximity to the marsh edge than elevation. In fact, when both elevation and edge were factors in the analysis, distributions of surface-dwelling Streblospio benedicti and crustaceans (primarily one species, Hargeria rapax) were often unrelated to elevation but almost always related to the marsh edge (Table 3). Even after removing elevation effects when significant, highest least square mean densities of these organisms remained within microhabitats nearest to the marsh edge (Table 3, Figure 12). These findings agree with those by Lin (1990) who found that ribbed mussels, also suspension feeders, were concentrated within a few meters of the marsh edge in a North Carolina salt marsh. On the Gulf coast of Florida, Subrahmanyam and Coultas (1980) also found Streblospio benedicti and Hargeria rapax to be more abundant in salt marsh habitats with lower surface elevations near the marsh edge. In Atlantic coast marshes,

Table 8.   Potential ecological factors controlling infaunal distributions consistent with a dominant edge effect versus a dominant elevation effect. Hypotheses that could be tested in support of each relationship are also shown.

Controlling Ecological Factor	Hypothesis

Distance from the marsh edge is dominant relationship

Food Availability	Distributions of feeding types will differ
Predation by Nekton	Distributions of most susceptible infauna will differ
	Seasonal differences in infaunal distribution will reflect seasonal changes in predator abundance
Sediment particle size	Infaunal species with strongest relationship to grain size will show strongest relationship
Recruitment	Infaunal species with planktonic recruits will show strongest relationship with edge
Sediment drainage, hypoxia, toxic sulfide concentrations	Most susceptible species show strongest relationship

Marsh surface elevation is dominant relationship

Desiccation	Strongest relationship will occur during periods of low water and high temperature
Temperature	Strongest relationships will occur during periods of temperature extremes
Predation by Nekton	Strongest relationships will occur during periods of high water when nekton have access to marsh

Streblospio benedicti is also abundant at lower elevations (Kneib 1984, Moy and Levin 1991), but densities of Hargeria rapax are often higher in the high intertidal zone (Reice and Stiven 1983; Kneib 1992). Surface dwelling species such as the polychaete, Streblospio benedicti and crustacean, Hargeria rapax generally showed a strong affinity for marsh-edge habitat, and the percentage of these suspension feeders and surface deposit feeders in relation to other feeding types decreased with increasing distance from the marsh edge.

Abundances of Capitella capitata, a near-surface deposit feeder, and Laeonereis culveri, an omnivorous species, had distribution patterns similar to those of surface dwellers; densities of these organisms within the marsh were highest at low elevations near the edge (Table 2). Analysis of covariance indicated that Capitella capitata was related to both distance from the marsh edge and elevation, and Laeonereis culveri was related to elevation differences in the microhabitats and not edge effects (Table 3). Generally, distributions of both species were more influenced by elevation than edge, especially during the spring and mid-summer when tidal inundation was low or variable.

In contrast to other infauna, the abundances of the most common subsurface direct deposit feeders, the oligochaetes, were not centered near the marsh edge (Table 2). In fact, mean oligochaete densities and the proportion of subsurface direct deposit feeders were frequently highest in areas farthest from the marsh edge. During April, October, and November sampling periods, there was a positive relationship between oligochaete abundance and elevation (Table 3). In contrast, oligochaete densities in North Carolina were highest in low and middle intertidal zones in adjacent

transplanted and natural salt marshes (Moy and Levin 1991). Kneib (1984) found that oligochaete densities were similar throughout the vegetated intertidal zone in an Atlantic salt marsh off Sapelo Island, Georgia.

Enhanced feeding efficiency near the marsh edge may explain why mean densities of most suspension and surface deposit feeders are highest near the edge (Table 1). Vegetation near the edge reduces water velocity and may increase settlement of suspended food particles, just as it increases settlement of sediments (Stumpf 1983; Warren and Niering 1993; Jadhav and Buchbergereco 1995). Peterson and Black (1987, 1988) found that growth rates of several species of marsh clams were inversely related to elevation in an Australian salt marsh. They found that reduced flooding duration at higher elevations did not fully explain the reduction in growth rates and suggested that clams at low elevations near the marsh edge filtered out most of the suspended food particles before the water could reach clams at higher elevations farther from the marsh edge. The unexplained differences in their growth rates, however, may also have been related to enhanced passive settlement of suspended food particles at low elevations near the marsh edge.

Another possible mechanism explaining edge effects within the marsh involves larval recruitment. Just as vegetation on the marsh edge may cause suspended food particles to settle, it may cause the passive settlement of planktonic larvae (Hannah 1984; Butman 1987; Eckman 1990). In addition, abundances in marsh edge habitat may be elevated if benthic infauna actively select settlement sites. Most larvae must traverse over the marsh edge to reach areas of the inner marsh thereby giving larva more of an opportunity to select edge habitat. Sediment grain size has often

been suggested as a criterion for a suitable habitat for many suspension feeding species (Johnson 1970; Flint and Kalke 1985), and experiments have shown that larva of many suspension feeding species often prefer to settle in areas characterized by large sediment grains which also indicate stronger currents (Meadows and Campbell 1972; Gray 1974). Marsh edge habitat had the largest average grain size of all vegetated microhabitats; therefore, suspension feeders may have actively selected marsh edge microhabitats for this reason. Although increased larval settlement near the marsh edge may be one explanation for the distributions of infauna, such as Streblospio benedicti, that undergo a planktonic larval stage; it does not explain the high marsh edge densities of many crustaceans, such as Hargeria rapax, that do not have planktonic larvae.

Although infaunal densities on the marsh edge were often highest within the vegetated marsh, densities of Streblospio benedicti, Capitella capitata, and Laeonereis culveri were often equally high in vegetated and nonvegetated areas one meter on either side of the marsh edge. In fact, highest densities of these three species were occasionally found in nonvegetated microhabitats (Figures 4-6). Similar densities in marsh edge and nonvegetated microhabitats suggest that these species may receive some benefit by just being near the marsh edge which seems to be unrelated to the function of refuge given by vegetative structure. However, hydrodynamic processes influenced by vegetative structure such as suspended particle settlement may extend out a short distance from the marsh edge.

The spatial distribution of most infauna on the marsh surface was often related to edge and elevation; however, the temporal patterns of infaunal abundance appear to be controlled by other factors. During the late

summer and early fall, densities of infauna fell dramatically in all intertidal microhabitats sampled and consequently, only a few differences in densities between microhabitats were detected by October. This seasonal decline was likely caused by a seasonal increase in predator density on the marsh during this time of the year. Numerous studies have shown that high predator densities during the late summer/early fall can significantly reduce the number of benthic infauna in Atlantic and Gulf coast salt marshes (Cammen 1976; Bell 1979; Subrahmanyam and Coultas 1980; Kneib and Stiven 1982; Subrahmanyam and Coultas 1980; Zimmerman et al. 1991). Therefore, any edge and elevation effects on infaunal abundance were probably overshadowed by intense predation pressure in all microhabitats during August and October when predators were most abundant, and marsh microhabitats were often flooded and accessible to these predators (Table 4).

Experiments performed by McTigue and Zimmerman (1991) suggest that nekton prefer epibenthic crustaceans and surface-dwelling polychaetes, and that densities of these organisms are reduced earlier in the year than other less accessible types of infauna. Mean densities of surface-dwelling crustaceans were reduced to near zero in many microhabitats by the August sampling period; by October, mean densities of several surface and near-surface dwelling species of polychaetes had also been reduced. In contrast, oligochaete densities remained relatively high during this period. In October, oligochaetes became the most abundant annelid and distribution patterns for total infauna mirror those for oligochaetes with highest densities farthest from the marsh edge. Oligochaetes may not be as affected

by predation because they burrow deeper than other types of subsurface deposit feeders.

Salt marshes have been shown in several studies to receive a small net influx of carbon from allochthonous sources (Erkenbrecher and Stevenson 1975; Woodwell et al. 1977; Rublee et al. 1983). Wolaver and Spurrier (1988) found that vegetated areas of the marsh were a sink for particulate organic matter during tidal inundation. The largest removal rate occurred when tidal water covered only the low marsh, characterized by the tall form of <u>Spartina</u> <u>alterniflora</u>. I suggest that marsh edge vegetation also traps allochthonous food particles that are then consumed by the relatively large number of suspension and surface deposit feeders found in these microhabitats. This process could enhance benthic productivity of marshes with a large amount of marsh edge habitat.

Increased benthic productivity could be transferred to nektonic predators whose densities have also been found to be higher in areas near the marsh edge (Lin 1989, 1990; Minello et al. 1991; Baltz et al. 1993; Kneib and Wagner 1994; Minello et al. 1994; Peterson and Turner 1994; Schindler et al. 1994). Minello et al. (1994) suggested that high concentrations of many nektonic predators found on the marsh edge may be related to similar distributions of benthic prey. In this study, I found that benthic infauna are concentrated in areas near the marsh edge. However, it is unknown whether the distribution of predators are affected by prey distribution or both predator and prey distributions are similarly affected by a third factor associated with marsh edge.

CHAPTER IV

RELATIVE VALUE OF BENTHIC INFAUNA WITHIN SALT MARSH MICROHABITATS TO NEKTON PREDATORS

Introduction

High densities of benthic infauna within salt marshes are an important source of food for many species of nekton living within estuaries of the Gulf and Atlantic coasts of the U. S. (Weisberg and Lotrich 1982; Minello and Zimmerman 1991). Recently, several studies have found that at high tide, when extensive intertidal habitat is available, more natant predators utilize marsh areas within a few meters the edge compared with inner marsh areas several meters away from the edge (Minello et al. 1991; Baltz et al. 1993; Kneib and Wagner 1994; Minello et al. 1994; Peterson and Turner 1994). This preference for the marsh edge may be caused by the presence of thicker vegetation, or a higher risk of stranding at low tide in areas away from the marsh edge (Gibson 1988; Lin 1989; Minello et al. 1994; Peterson and Turner 1994; Schindler et al. 1994). However, greater food benefits in areas near the marsh edge may also play a role.

My field investigation found that infaunal abundance was significantly higher within one meter of the marsh edge compared to vegetated areas three, five, and ten meters from the nearest edge for most of the year in Gang's Bayou. Infaunal densities, however, provide only limited information on the availability of benthic infauna to predators and the trophic relationship between infaunal prey and marsh predators. I performed growth experiments to determine if these higher densities of

infaunal prey on the marsh edge translate into higher growth rates for predators using this microhabitat.

Methods

Predator growth was measured in the laboratory to determine the relative value of infaunal populations within marsh sediments as sources of food. Large sediment cores were randomly extracted from three microhabitats within the sampling area: nonvegetated mudflat (1 M downslope from the marsh edge), marsh 1 meter from edge, and marsh 10 meters from the marsh edge. Thirty cylindrical chambers (20.3-cm diameter and 30-cm height) were used to collect the marsh sediments (15-cm deep) and associated biota from each of the three microhabitats. The chambers were transported to the laboratory in individual buckets and put into a flow-through water table. Vegetation was clipped at 15 cm and mesh lids were placed over the chambers to reduce the chance of the predators escaping. The predators were placed individually in the chambers and allowed to forage on enclosed sediments for a two-week period.

To ensure adequate circulation and availability of dissolved oxygen, aerated sea water was supplied to each individual chamber from a common reservoir through individual plastic tubes at a rate of approximately 300 ml per hour. A 200-μm mesh lid on each chamber allowed water to flow out the top of each chamber but prevented experimental organisms from escaping. Sea water used in the system was pumped from the front beach off Galveston Island and filtered through sand and a 200-μm mesh to avoid adding extraneous food. A Hydrolab Datasonde placed in the water table measured water temperature and salinity every hour throughout the

experiments. Water salinities in the laboratory were similar to salinities at the marsh study area. Light in the laboratory was provided by daylight fluorescent bulbs on a 12-h light and 12-h dark cycle and ranged in brightness from 1.5 to 6.0 µEinsteins s^{-1} m^{-2} in the individual chambers.

Each experiment compared the growth of two predator species (10 replicate chambers each) foraging on sediments taken from three microhabitats. In addition to these 60 experimental chambers, 10 chambers per microhabitat served as controls. Five control chambers per microhabitat did not have predators and were used to determine if infaunal mortality unrelated to predation by experimental animals varied among microhabitat treatments. Small cores (5-cm diameter) were extracted from these chambers at the initiation of the experiment. These small cores were extracted from all control and experimental chambers again at the end of the experiment. The remaining five control chambers per transect included brown shrimp, and additional food (commercial fish pellets) was added ad libitum to these chambers each day during the experimental period. Predator growth in these chambers was used to determine if growth was food-limited and if there was any difference in growth between microhabitat treatments not related to the availability of food. Each of the 90 chambers (3 microhabitat treatments x 2 predators x 10 replicates + 3 microhabitat treatments x 10 controls) were placed at random locations in the water table.

Predators were collected before each experiment by seining near the sampling area. Predators were acclimated to laboratory conditions in large fiberglass holding tanks and fed commercial fish pellets for one week before the experiment. At the initiation of the experiment, predators were randomly assigned to experimental and control chambers. Growth was determined by comparing live weight and total length of predators at the

initiation of the experiment and again after the two week experimental period. Two experiments were conducted, each involving two common marsh predators. In the late spring (May-June), the predators were gulf killifish, Fundulus grandis (46-58 mm TL) and brown shrimp Penaeus aztecus (28-58 mm TL). In the summer (August-September) experiments, white shrimp Penaeus setiferus (32-41 mm TL) and brown shrimp (36-42 mm TL) were used as predators. The timing of experiments coincided with the two main annual pulses of predators into Gulf Coast marshes (Zimmerman and Minello 1984).

Statistical Analyses

Daily growth of experimental predators (in total length and biomass) was analyzed with a two-way Analysis of Variance (ANOVA) using Type III sums of squares to adjust for unbalanced cell size (SuperANOVA statistical package, Abacus Concepts, Inc., Berkeley, CA, 1989). The number of observations for each treatment combination in the analyses is shown in Table 9. The main effects in the ANOVAs were the microhabitat where the sediment was collected (n=3) and the predator species (n=2). The main null hypothesis of interest was that growth rates were equal in all three microhabitats. An F-max test (Milliken and Johnson 1984) was used to test for homogeneity of variance at the 0.05 significance level. Growth rates measured in length and biomass were significantly heteroscedastic for both experiments. A logarithmic transformation corrected this heteroscedasticity

Table 9.   Number of successful observations for three microhabitats and treatment combinations for spring and summer growth experiments in 1995. The three microhabitats that were tested were nonvegetated intertidal, one meter downslope of the marsh edge (shown here as -1 M), and vegetated marsh areas one (1 M) and ten meters (10 M) from the marsh edge.

Spring

Microhabitat	Brown Shrimp	Gulf Killifish	Control 1: Infaunal mortality	Control 2: Brown shrimp fed	Sum
-1 M	10	8	5	5	28
1 M	10	8	5	5	28
10 M	10	9	5	5	29

Total number: 85

Summer

Microhabitat	Brown Shrimp	White Shrimp	Control 1: Infaunal mortality	Control 2: Brown shrimp fed	Sum
-1 M	9	9	5	5	28
1 M	6	8	5	5	24
10 M	7	6	5	5	23

Total number: 75

in the spring analysis, while a square root transformation corrected the problem in the summer analysis.

Initial and final infaunal densities and biomass were tested for differences among microhabitats using a one-way ANOVA after transforming abundance data using a $L_n(x+1)$ transformation. The number and biomass of infauna removed by experimental predators were calculated by subtracting the infaunal densities and biomass in each experimental chamber from the mean densities and biomass of infauna in control chambers for each microhabitat at the end of the experiment. These new variables represented infauna missing or removed from sediments over the 14-day experimental period. A two-way ANOVA was calculated using these variables as observations and comparing microhabitats and predator species. The above analyses were conducted on the total number of infauna, annelids, polychaetes, Capitella capitata, Streblospio benedicti, Laeonereis culveri, oligochaetes, crustaceans, annelid biomass, and crustacean biomass.

Spring Experiment Results

Physical and Chemical Conditions

When sediments were collected for the spring experiment (May 24-June 6), salinities ranged from 17 to 20 ppt at the sampling area near Gang's Bayou. In the laboratory, the mean salinity over the experimental period was 25 ppt (range = 25 ppt to 26 ppt) and the mean temperature during the experiment was 25°C (range = 23.4°C to 25.5°C).

Growth

Overall mean growth for brown shrimp was 0.2 mm TL/day (SE= 0.03); whereas mean growth rates for gulf killifish were near zero (Figure 15). Growth in biomass averaged 3.7 mg/day (SE= 1.36) for brown shrimp, and over the 14 days mean biomass increased for this species by 20.2% (Figure 16). Brown shrimp in control chambers with added food had much higher growth rates averaging 0.5 mm TL/day (SE=0.06) and 30.1 mg/day (SE=0.06). For gulf killifish, daily growth was negative and the fish lost an average of 14.4 mg/day (SE=2.41); the mean decrease in biomass over the 14 days was 13.1%. There were no significant differences in predator growth measured in biomass or length among microhabitats (Figures 15 and 16, Table 10).

Infauna Removed from Sediments

Infauna from the sediments collected for the spring experiment were dominated by polychaetes (70% of total), primarily Capitella capitata, Streblospio benedicti, and Laeonereis culveri (Table 11). Field densities of infauna two weeks prior to the experiment were fairly similar to initial densities in control chambers for the nonvegetated (-1 M) and inner marsh (10 M) microhabitats (Figure 17). In the edge microhabitat, however, there was a large decline over this period from field densities of total infauna (Figure 17) and of Streblospio benedicti, oligochaetes, crustaceans, and crustacean biomass in particular (Figures 18-21). For Capitella capitata, Laeonereis culveri, and annelid biomass these differences were negligible (Figures 22-24). Because of this decline, comparisons of initial control densities indicated no significant differences among microhabitats (Table 12).

Figure 15.   Daily change in total length of brown shrimp and gulf killifish in experimental chambers and brown shrimp in control chambers that were fed additional food over the 14 days of the spring experiment. Error bars indicate one standard error.
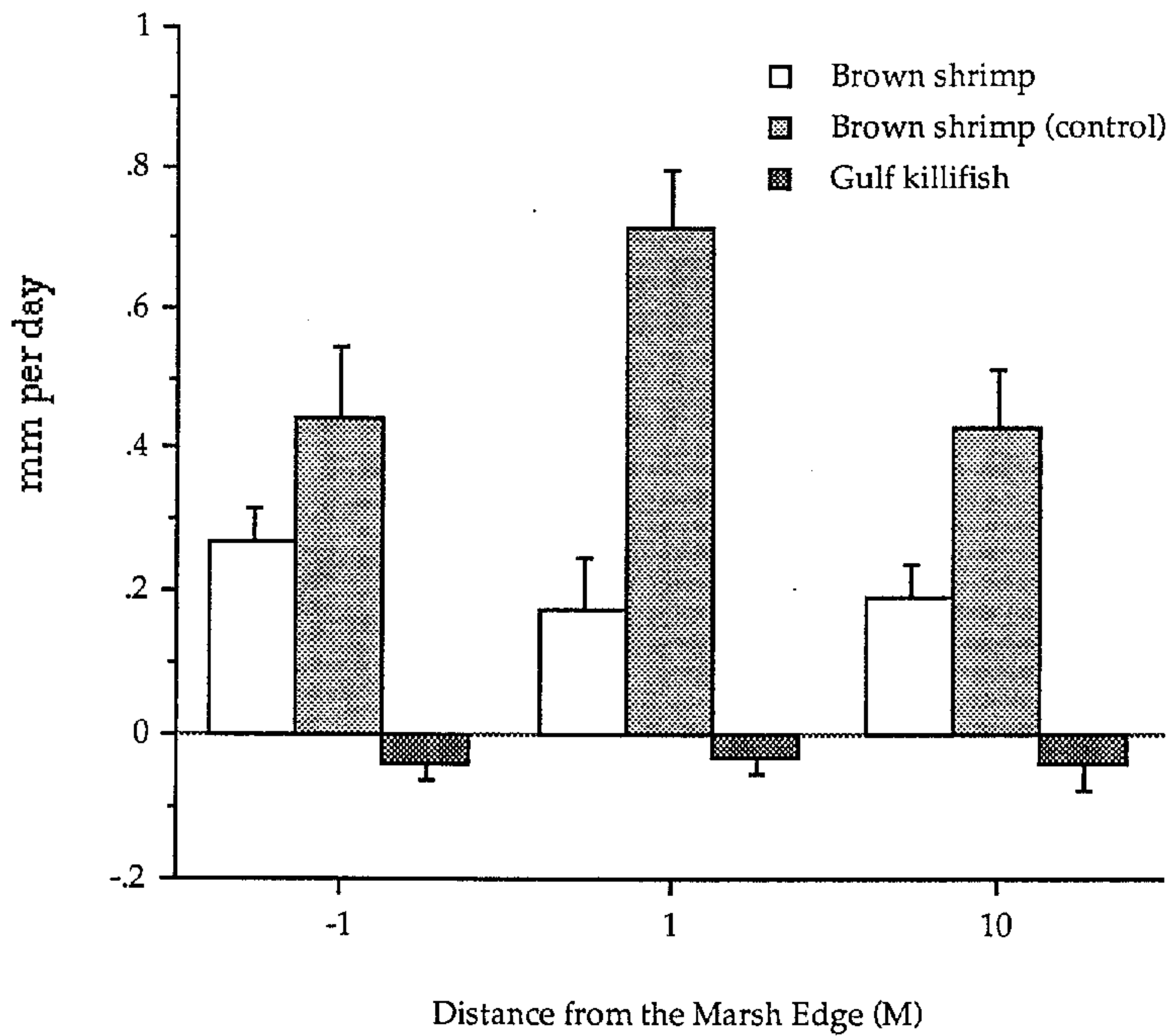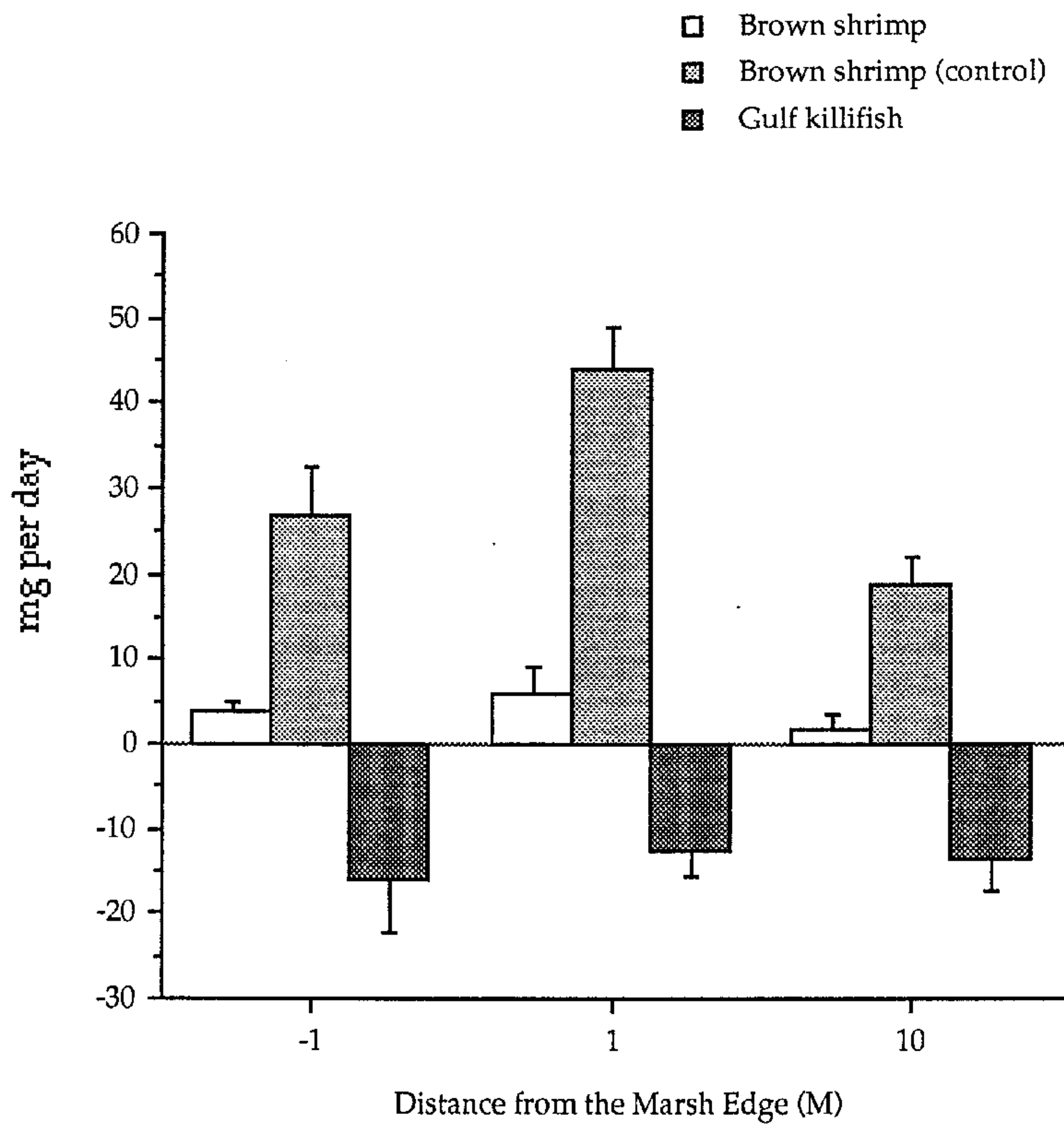
Figure 16 .   Daily change in biomass of brown shrimp and gulf killifish in experimental chambers and brown shrimp in control chambers that were fed additional food over the 14 days of the spring experiment. Error bars indicate one standard error.

Table 10.   Analysis of variance results for growth of predators during the spring experiment. Growth was analyzed by daily change in length (mm) and biomass (mg) which were transformed using $Ln(x+1)$. *A priori* contrasts within the predator term were used to compare the growth of brown shrimp in experimental chambers to those in control chambers that were fed additional food, and the growth of each species of predator.

Length (mm):

Source	df	SS	MS	F	P
Distance to Edge (microhabitat)	2	0.032	0.016	1.265	0.2904
Predator	2	1.858	0.929	74.196	0.0001
Predator*Distance to Edge	4	0.121	0.030	2.409	0.0602
Residual	55	0.689	0.013		
Contrasts:					
Experimental brown shrimp vs. Control brown shrimp (fed)	1	0.484	0.484	38.645	0.0001
Experimental brown shrimp vs. gulf killifish	1	0.607	0.607	48.512	0.0001

Biomass (mg):

Source	df	SS	MS	F	P
Distance to Edge (microhabitat)	2	3.063	1.532	0.915	0.4065
Predator	2	299.962	149.981	89.603	0.0001
Predator*Distance to Edge	4	2.781	0.695	0.415	0.7969
Residual	55	92.062	1.674		
Contrasts:					
Experimental brown shrimp vs. Control brown shrimp (fed)	1	51.488	51.488	30.761	0.0001
Experimental brown shrimp vs. gulf killifish	1	129.538	129.538	77.390	0.0001

Table 11.   Mean infaunal abundance and biomass (mg) values in control and experimental chambers in spring 1995 predation experiment (all microhabitats combined). Benthic infauna were sampled using a 19.6 cm^2 core, and these numbers were extrapolated to mean number per chamber (323.6 cm^2, standard error is also shown). Control chambers contained no predators. Initial cores were collected when predators were placed into experimental chambers. Final control cores and experimental (with predator) cores were collected following the 14-day experimental period.

	Initial control (N=15)		Final control (N=15)		Gulf killifish (N=25)		Brown shrimp (N=30)	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Total Infauna	555.9	(83.39)	785.5	(87.51)	582.1	(78.28)	609.2	(79.27)
Annelida	519.7	(79.93)	684.5	(76.47)	524.1	(66.58)	559.2	(70.86)
Polychaeta	445.0	(67.24)	516.4	(56.20)	392.2	(45.48)	434.0	(55.87)
Capitella capitata	217.5	(43.34)	238.4	(41.53)	202.4	(22.74)	186.8	(23.73)
Streblospio benedicti	143.9	(33.62)	163.7	(30.16)	121.3	(27.69)	189.5	(34.77)
Laeonereis culveri	72.5	(20.60)	78.0	(20.27)	51.4	(7.09)	44.5	(7.67)
Sabella sp.	6.6	(3.53)	13.2	(10.88)	2.6	(1.98)	5.5	(3.63)
Melinna maculata	3.3	(2.31)	9.9	(4.12)	4.0	(1.48)	4.4	(1.65)
Leitoscoloplos foliosus	0.0	(0.00)	12.1	(6.10)	6.6	(2.97)	0.0	(0.00)
Polydora ligni	0.0	(0.00)	1.1	(1.10)	2.0	(1.10)	1.6	(1.15)
Marphysa sanguinea	0.0	(0.00)	0.0	(0.00)	1.3	(0.99)	1.6	(0.99)
Eteone heteropoda	1.1	(1.10)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)
Scolelepis texana	0.0	(0.00)	0.0	(0.00)	0.7	(0.66)	0.0	(0.00)
Oligochaeta	74.7	(22.41)	168.1	(34.94)	131.8	(27.36)	125.2	(25.71)

Table 11.   Continued

	Initial control (N=15)		Final control (N=15)		Gulf killifish (N=25)		Brown shrimp (N=30)	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Crustacea	35.2	(11.21)	82.4	(18.95)	46.8	(14.83)	31.9	(8.73)
Hargeria rapax	15.4	(6.92)	48.3	(14.50)	22.4	(10.88)	19.2	(7.91)
Gammarus sp.	9.9	(6.76)	9.9	(4.45)	8.6	(4.45)	7.1	(3.30)
Corophium sp.	2.2	(1.48)	12.1	(4.61)	11.2	(5.93)	2.7	(1.32)
Grandidierella bonnieroides	6.6	(3.96)	9.9	(4.78)	3.3	(2.14)	1.1	(0.82)
Edotea montosa	0.0	(0.00)	0.0	(0.00)	1.3	(1.32)	1.1	(0.82)
Ampelisca sp.	1.1	(1.15)	0.0	(0.00)	0.0	(0.00)	0.5	(0.49)
Cl. Copepoda	0.0	(0.00)	2.2	(1.48)	0.0	(0.00)	0.0	(0.00)
Mollusca	0.0	(0.00)	3.3	(1.81)	1.3	(0.99)	1.6	(0.99)
Acteocina canaliculata	0.0	(0.00)	3.3	(1.81)	0.7	(0.66)	1.6	(0.99)
Chione cancellata	0.0	(0.00)	0.0	(0.00)	0.7	(0.66)	0.0	(0.00)
Other	1.1	(1.15)	15.4	(11.04)	9.9	(4.78)	16.5	(7.91)
Insect Larvae	1.1	(1.15)	15.4	(11.04)	9.9	(4.78)	10.4	(6.10)
Anemone	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	6.0	(5.44)
Infaunal Biomass (mg)	107.2	(23.07)	83.4	(14.83)	56.8	(4.94)	71.4	(8.24)
Annelid biomass (mg)	105.5	(23.07)	74.1	(11.54)	54.4	(4.94)	67.1	(8.24)
Crustacean biomass (mg)	2.4	(1.65)	2.9	(1.65)	1.8	(0.00)	2.3	(0.00)
Other biomass (mg)	0.0	(0.00)	6.5	(4.94)	0.6	(0.00)	2.0	(1.65)

Figure 17.   Mean densities of total infauna in three microhabitats from sediment cores (N=25) taken from the marsh two weeks prior to the initiation of the spring experiment and in the control and experimental chambers (see Table 9 for experimental Ns). Control chambers contained no predators. Initial cores were collected when predators were placed into experimental chambers. Final control cores and experimental (with predators) cores were collected following the 14-day experimental period. Each core had a surface area of 19.6 cm² and a depth of 5 cm. Error bars represent one standard error.

Figure 18.   Mean densities of Streblospio benedicti in three microhabitats from sediment cores (N=25) taken from the marsh two weeks prior to the initiation of the spring experiment and in the control and experimental chambers (see Table 9 for experimental Ns). Control chambers contained no predators. Initial cores were collected when predators were placed into experimental chambers. Final control cores and experimental (with predators) cores were collected following the 14-day experimental period. Each core had a surface area of 19.6 cm² and a depth of 5 cm. Error bars represent one standard error.
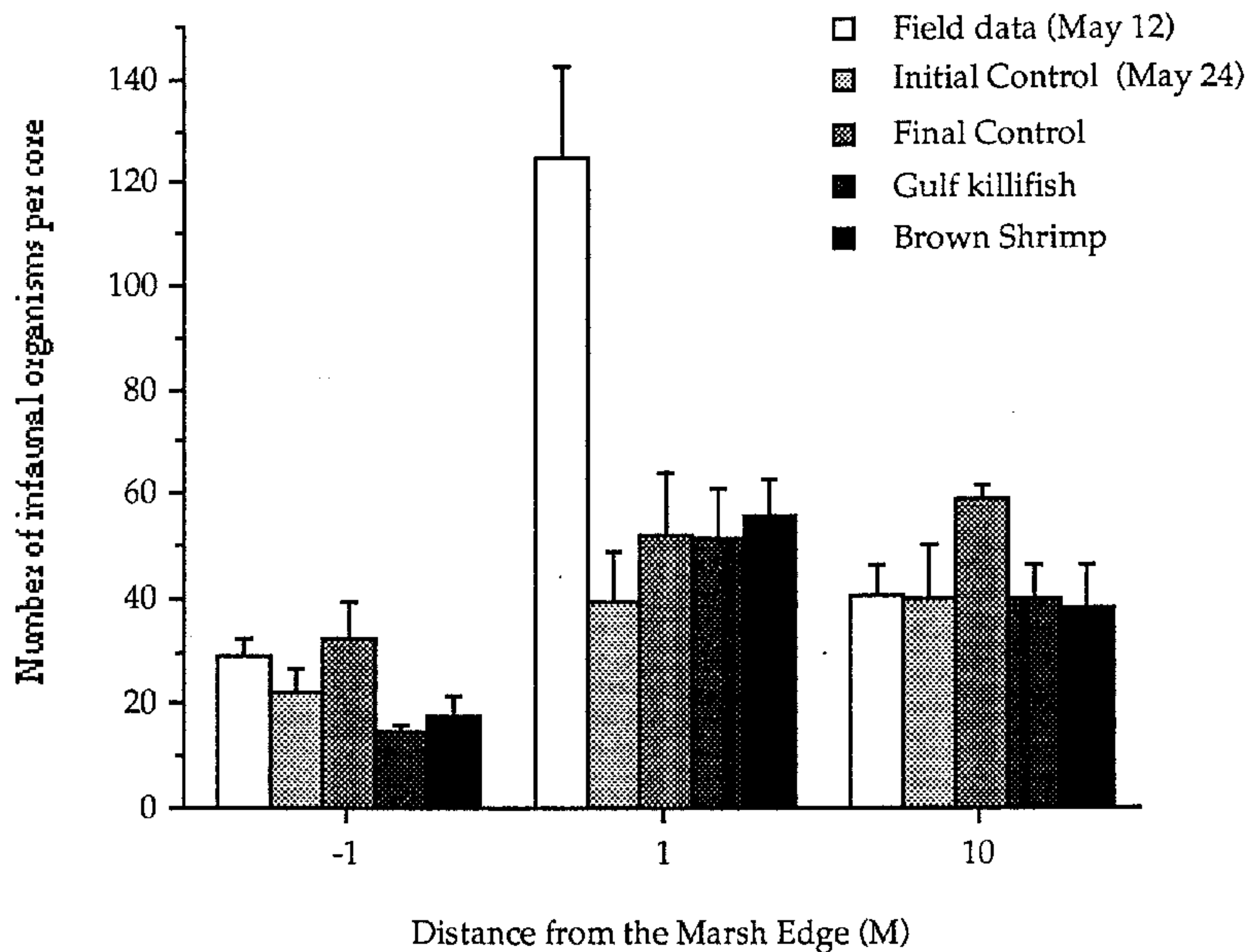
Figure 19.   Mean densities of oligochaetes in three microhabitats from sediment cores (N=25) taken from the marsh two weeks prior to the initiation of the spring experiment and in the control and experimental chambers (see Table 9 for experimental Ns). Control chambers contained no predators. Initial cores were collected when predators were placed into experimental chambers. Final control cores and experimental (with predators) cores were collected following the 14-day experimental period. Each core had a surface area of 19.6 cm^2 and a depth of 5 cm. Error bars represent one standard error.
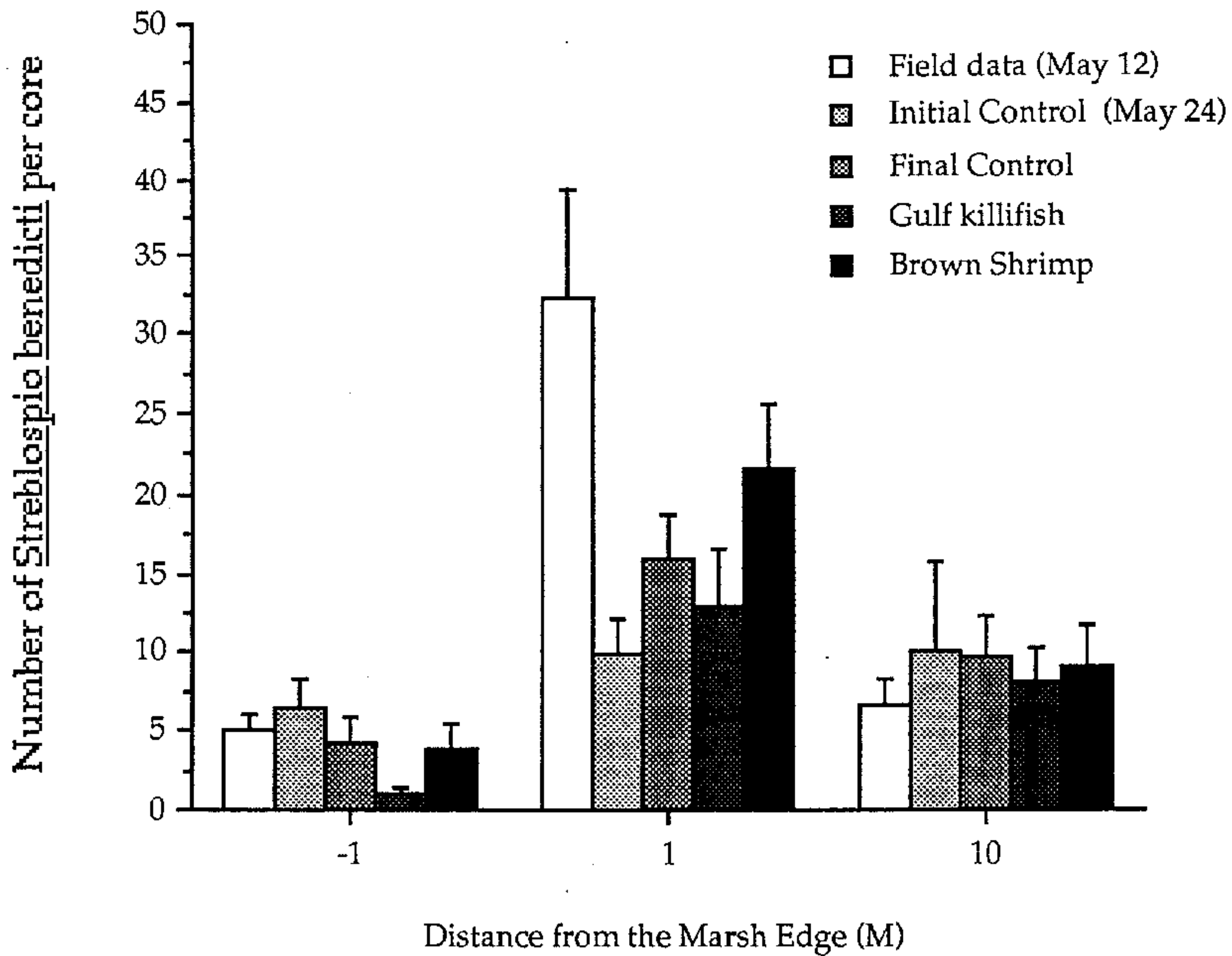
Figure 20.   Mean densities of crustaceans in three microhabitats from sediment cores (N=25) taken from the marsh two weeks prior to the initiation of the spring experiment and in the control and experimental chambers (see Table 9 for experimental Ns). Control chambers contained no predators. Initial cores were collected when predators were placed into experimental chambers. Final control cores and experimental (with predators) cores were collected following the 14-day experimental period. Each core had a surface area of 19.6 cm^2 and a depth of 5 cm. Error bars represent one standard error.
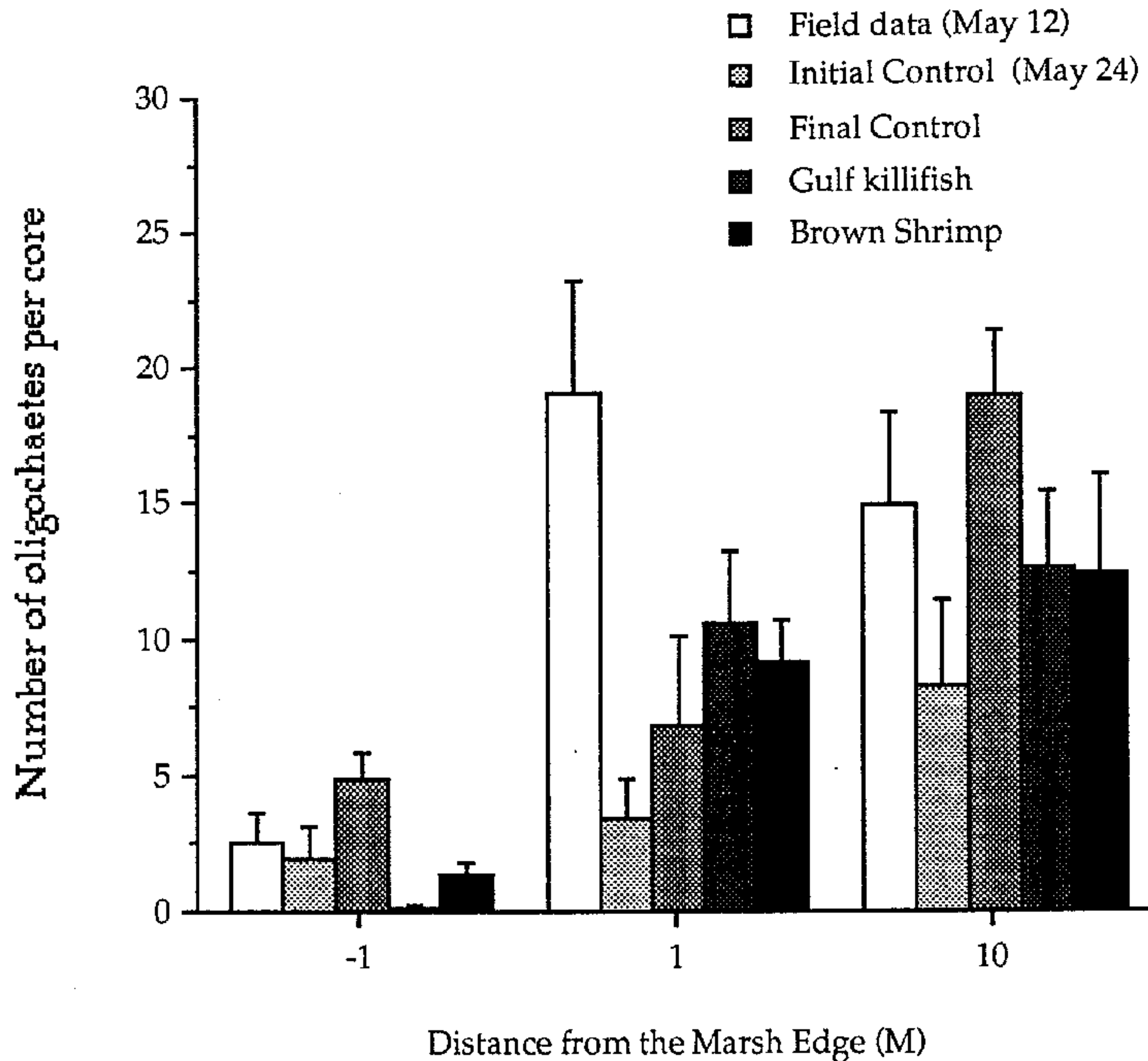
Figure 21. Mean crustacean biomass (mg) in three microhabitats from sediment cores (N=25) taken from the marsh two weeks prior to the initiation of the spring experiment and in the control and experimental chambers (see Table 9 for experimental Ns). Control chambers contained no predators. Initial cores were collected when predators were placed into experimental chambers. Final control cores and experimental (with predators) cores were collected following the 14-day experimental period. Each core had a surface area of 19.6 cm^2 and a depth of 5 cm. Error bars represent one standard error.
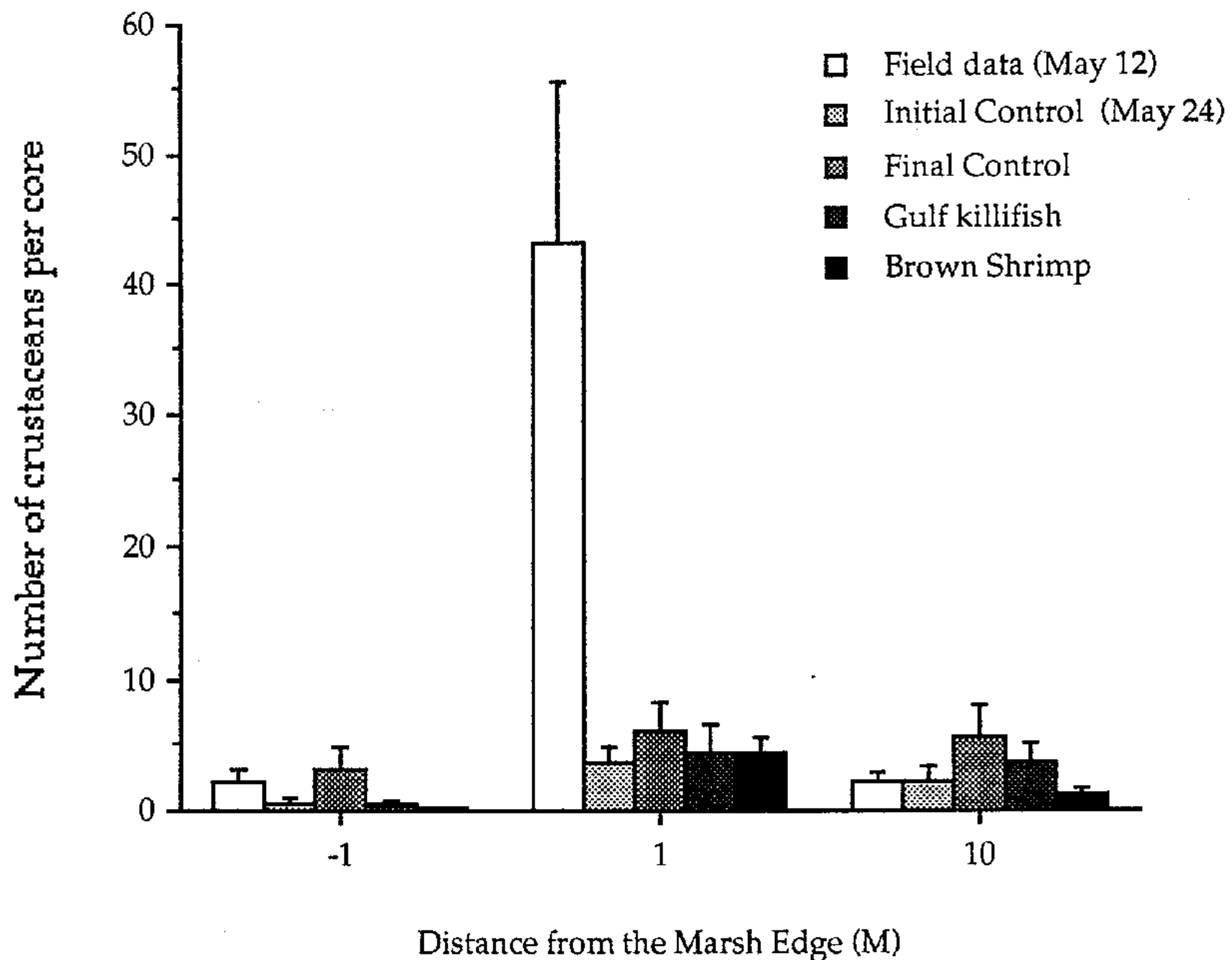
Figure 22.   Mean densities of <u>Capitella</u> <u>capitata</u> in three microhabitats from sediment cores (N=25) taken from the marsh two weeks prior to the initiation of the spring experiment and in the control and experimental chambers (see Table 9 for experimental Ns). Control chambers contained no predators. Initial cores were collected when predators were placed into experimental chambers. Final control cores and experimental (with predators) cores were collected following the 14-day experimental period. Each core had a surface area of 19.6 cm² and a depth of 5 cm. Error bars represent one standard error.
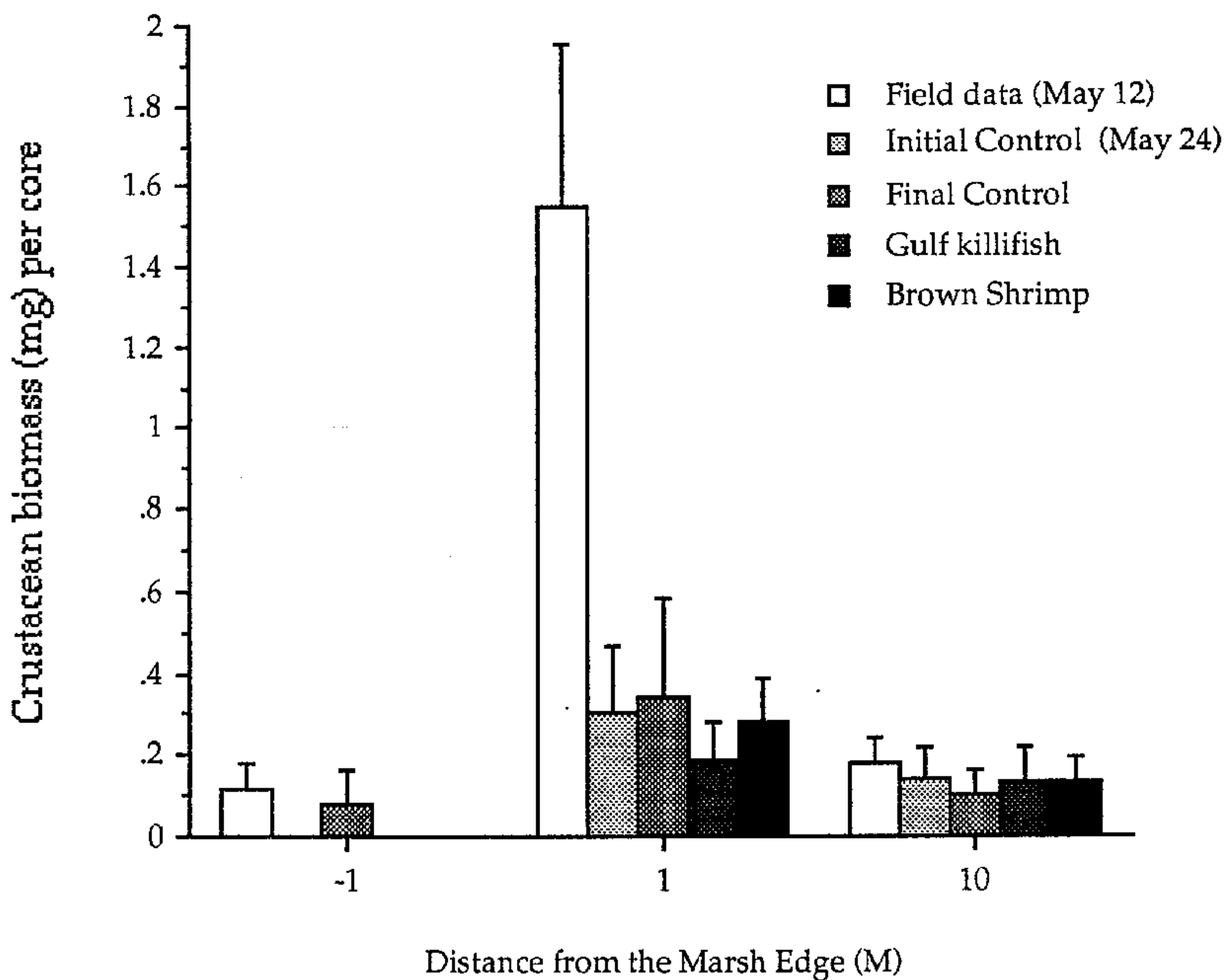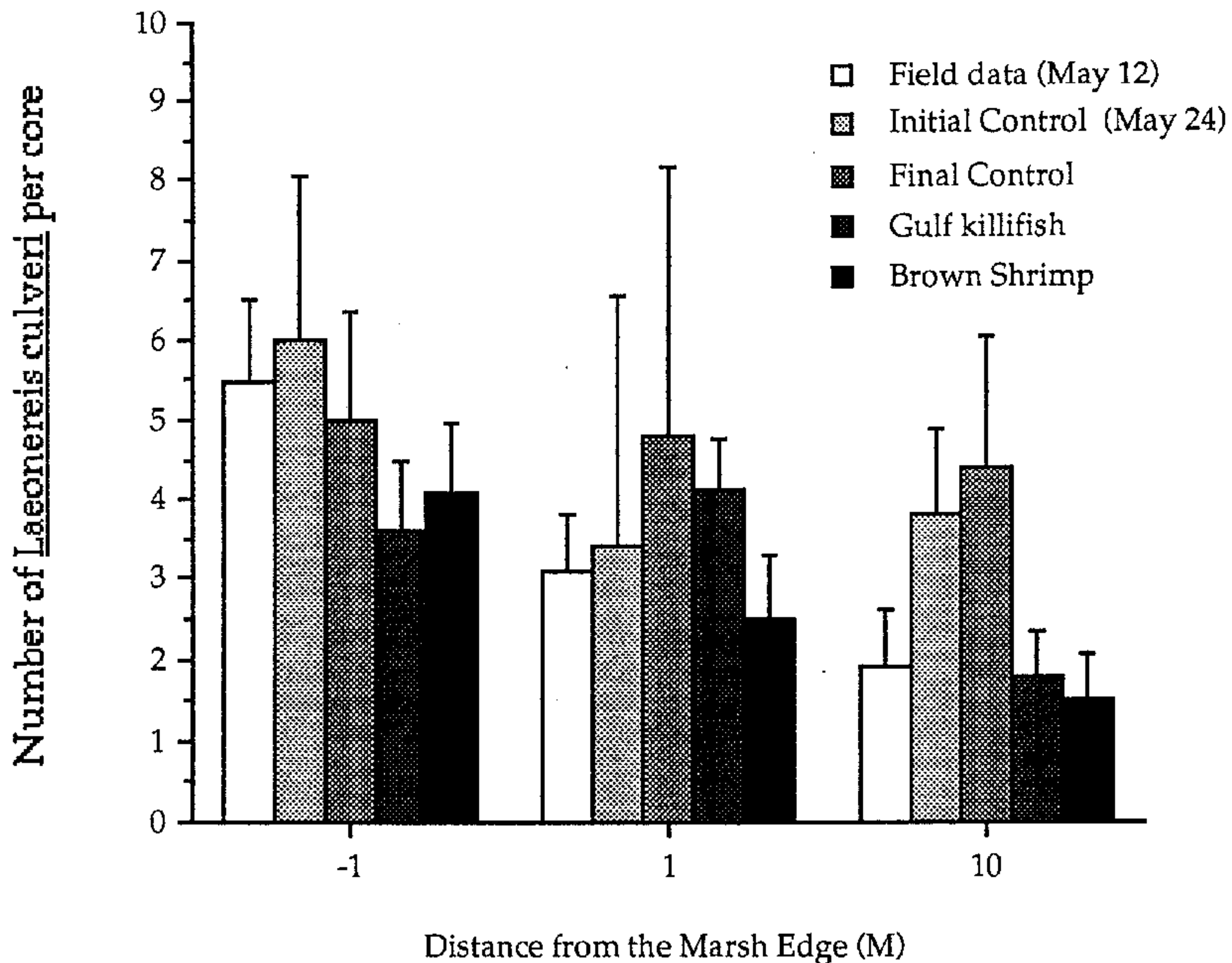
Figure 23.   Mean densities of Laeonereis culveri in three microhabitats from sediment cores (N=25) taken from the marsh two weeks prior to the initiation of the spring experiment and in the control and experimental chambers (see Table 9 for experimental Ns). Control chambers contained no predators. Initial cores were collected when predators were placed into experimental chambers. Final control cores and experimental (with predators) cores were collected following the 14-day experimental period. Each core had a surface area of 19.6 cm^2 and a depth of 5 cm. Error bars represent one standard error.
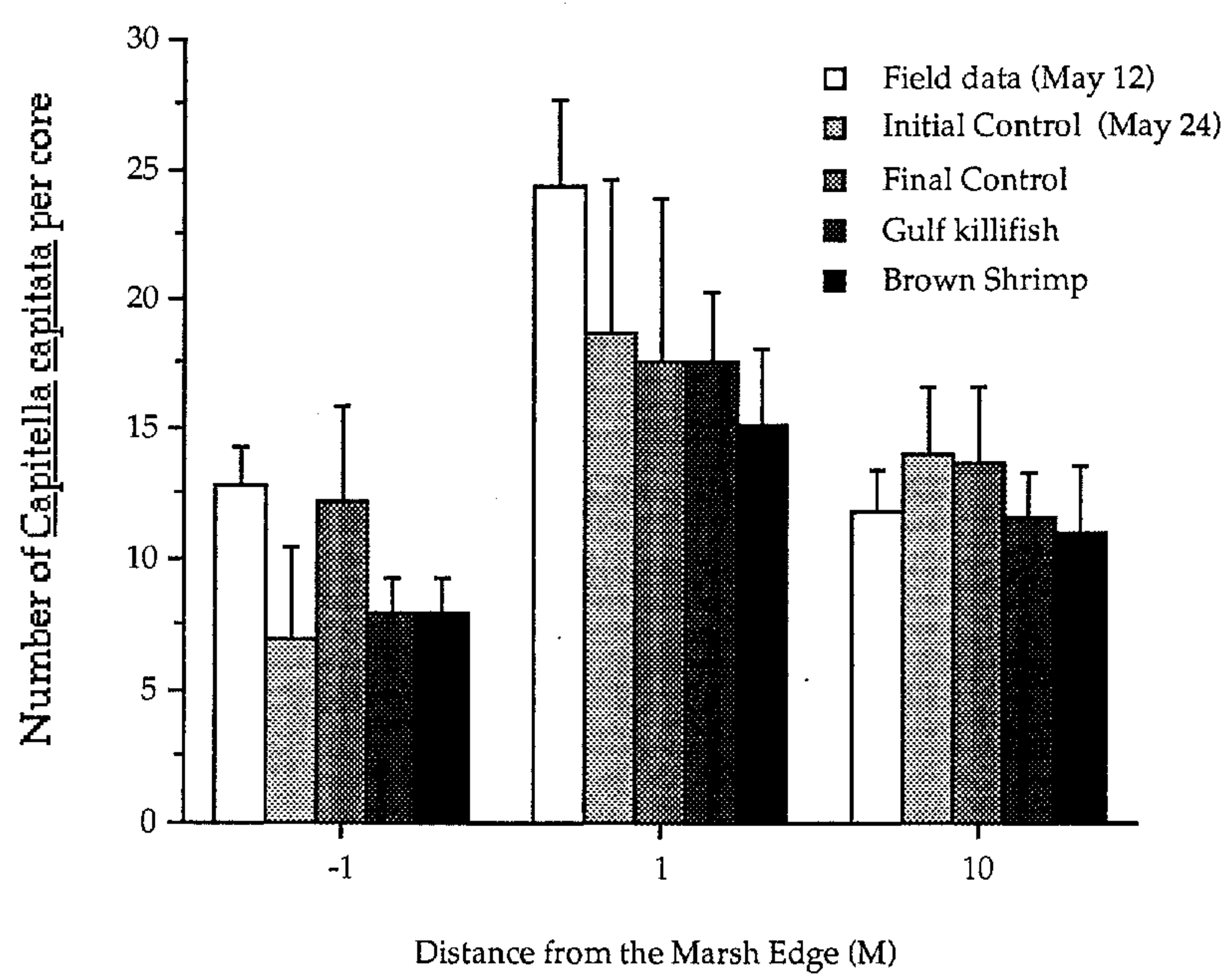
Figure 24. Mean annelid biomass(mg) in three microhabitats from sediment cores (N=25) taken from the marsh two weeks prior to the initiation of the spring experiment and in the control and experimental chambers (see Table 9 for experimental Ns). Control chambers contained no predators. Initial cores were collected when predators were placed into experimental chambers. Final control cores and experimental (with predators) cores were collected following the 14-day experimental period. Each core had a surface area of 19.6 cm^2 and a depth of 5 cm. Error bars represent one standard error.
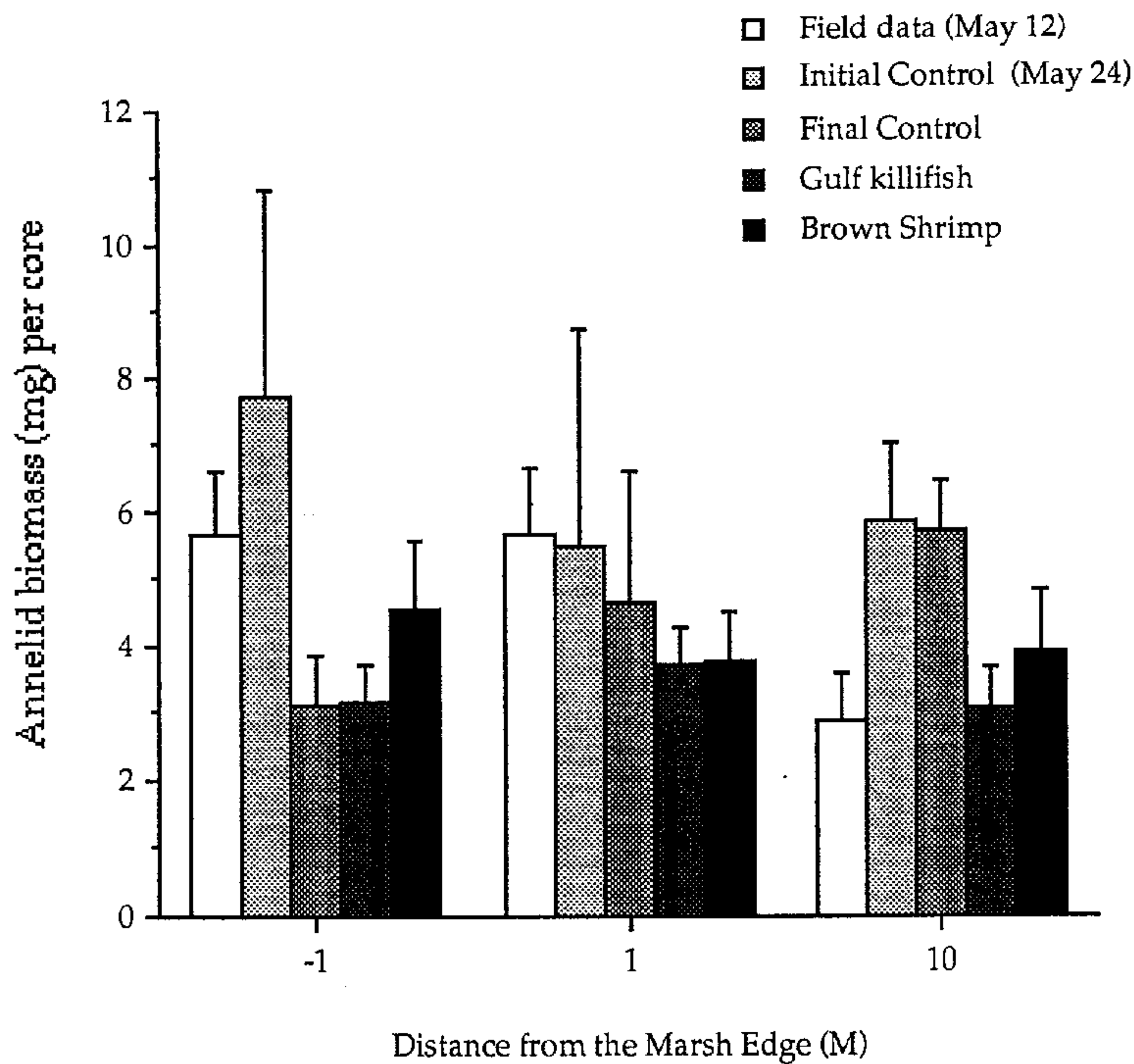
Table 12.   Results from one-way ANOVA's testing the main effect of edge on initial and final infaunal densities in control chambers. Degrees of freedom are total (14), main effect of Edge (2), and residual error (12). Data were transformed using $L_n(x+1)$.

SPRING EXPERIMENT	Main Effect of Edge Initial densities		Main Effect of Edge Final densities	
Dependent variable:	SS	P-value	SS	P-value
Total infauna	0.865	0.2903	1.343	0.0536
Annelids	0.655	0.4374	1.068	0.1011
Polychaetes	0.454	0.5178	0.672	0.2170
Capitella capitata	3.340	0.5178	0.278	0.7774
Streblospio benedicti	0.538	0.6513	4.216	0.0303
Laeonereis culveri	2.543	0.2916	0.713	0.6703
Oligochaetes	2.637	0.2750	4.989	0.0031
Crustaceans	2.084	0.2279	1.084	0.5343
Annelid biomass (mg)	0.534	0.6431	0.790	0.3460
Crustacean biomass (mg)	0.134	0.1666	0.088	0.4545

SUMMER EXPERIMENT	Main Effect of Edge Initial densities		Main Effect of Edge Final densities	
Dependent variable:	SS	P-value	SS	P-value
Total infauna	0.527	0.8172	1.112	0.2520
Annelids	0.632	0.7940	1.310	0.2722
Polychaetes	3.285	0.3003	0.316	0.7785
Capitella capitata	0.836	0.5066	4.154	0.0853
Streblospio benedicti	3.482	0.0901	0.611	0.4381
Laeonereis culveri	2.227	0.2283	0.792	0.5027
Oligochaetes	2.726	0.3729	1.610	0.2024
Crustaceans	0.064	0.3966	0.448	0.1005
Annelid biomass (mg)	5.410	0.0637	0.734	0.3388
Crustacean biomass (mg)	-	-	-	-

Final mean densities of overall infauna and the most common taxa were generally lower in chambers with predators than in control chambers in the nonvegetated (-1 M) and inner marsh (10 M) microhabitats (Figures 17-24). However, when data from microhabitats were combined (Table 11), analysis of variance revealed that there were no significant differences in overall infaunal abundance among any of the experimental and control treatments (df=3, SS=2.9, MS=0.7, f=1.5,p=0.20). The number and biomass of prey removed by predators was analyzed for Microhabitat (Distance to Edge) effects, and predators removed significantly fewer numbers and lower biomass of infauna from the edge microhabitat than from inner marsh microhabitats (Table 13, Figures 25 and 26). Predators removed fewer infauna but a higher biomass from the edge compared to the nonvegetated microhabitat.

Summer Experiment Results

Physical and Chemical Conditions

When sediments were collected for the summer experiment (August 30 - September 13), salinities ranged from 21 to 25 ppt at the sampling area near Gang's Bayou. In the laboratory, the mean salinity over the experimental period was 28.5 ppt (range = $28.3^{\circ}C$ to $29.6^{\circ}C$) and the mean temperature during the experiment was $28.6^{\circ}C$ (range = $25.3^{\circ}C$ to $29.5^{\circ}C$).

Growth

Mean white shrimp growth was 0.1 mm TL/day (SE = 0.2) and 1.0 mg/day (SE=1.2). The mean increase in biomass over the 14 days was 4.3%. For brown shrimp, mean growth was 0.1 mm TL/day (SE= 0.03) and

Table 13.   Results of two-way analysis of variance for number/biomass of infauna removed by predators in experimental chambers in spring 1995. *A priori* contrasts within the Distance to Edge (microhabitat) term were used to compare the number/biomass of infauna removed in the marsh edge microhabitat (1 M) to those in the nonvegetated (-1 M) and inner marsh (10 M) microhabitats.

Infauna   Abundance

Source	df	F	P
Distance to Edge	2	4.214	0.0212
Predator	1	0.193	0.6622
Predator*Distance to Edge	2	0.186	0.8311
Residual	44		

Contrasts:

-1 M vs. 1 M	1	3.894	0.0548
1 M vs. 10 M	1	7.969	0.0071

Infauna   Biomass   (mg)

Source	df	F	P
Distance to Edge	2	15.320	0.0001
Predator	1	3.345	0.0742
Predator*Distance to Edge	2	1.072	0.3510
Residual	44		

Contrasts:

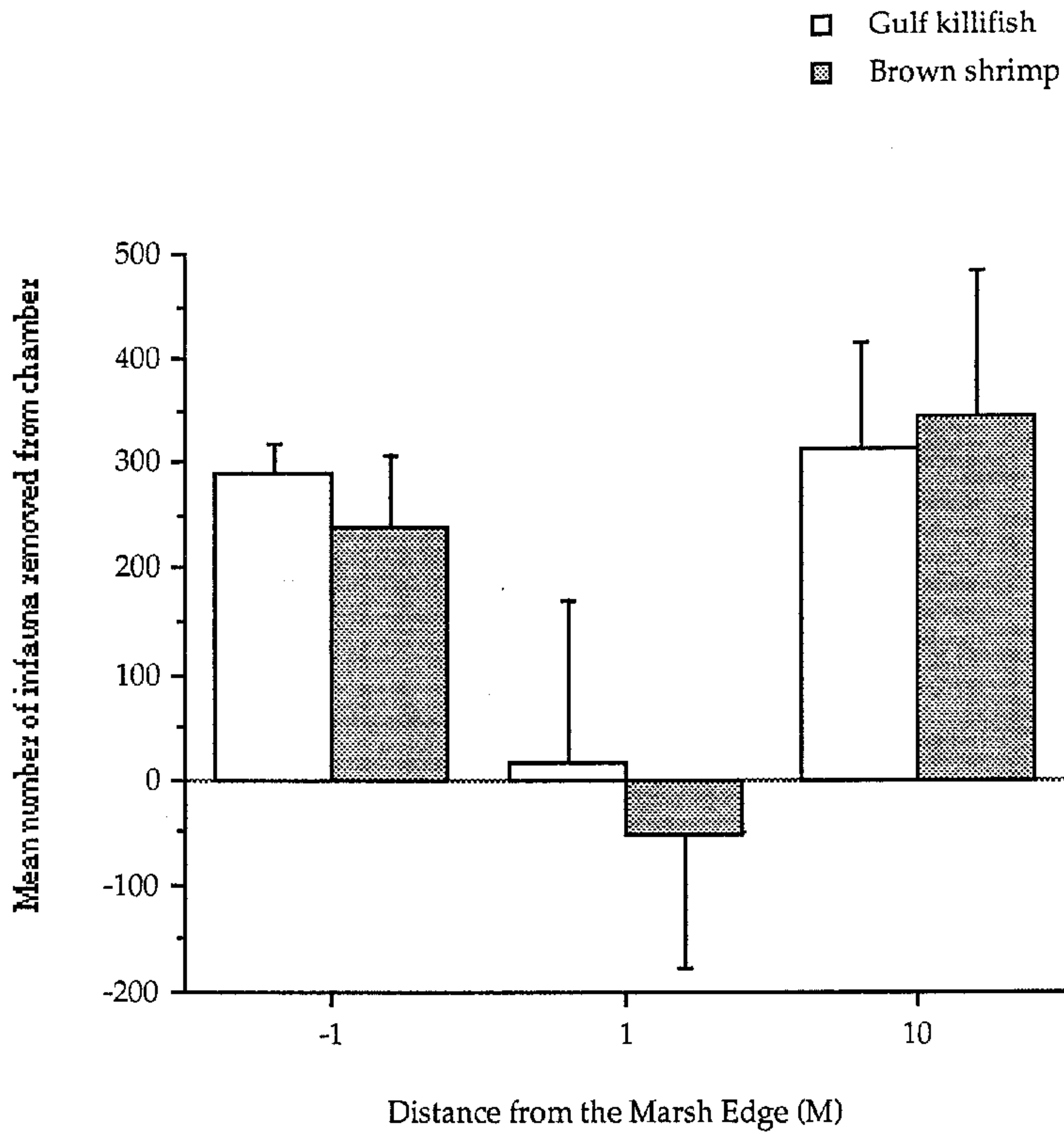|			
-1 M vs. 1 M	1	1.348	0.0095
1 M vs. 10 M	1	8.294	0.0061

Figure 25 .   Mean number of total infauna removed by predators from experimental chambers during the spring experiment. Error bars represent one standard error.
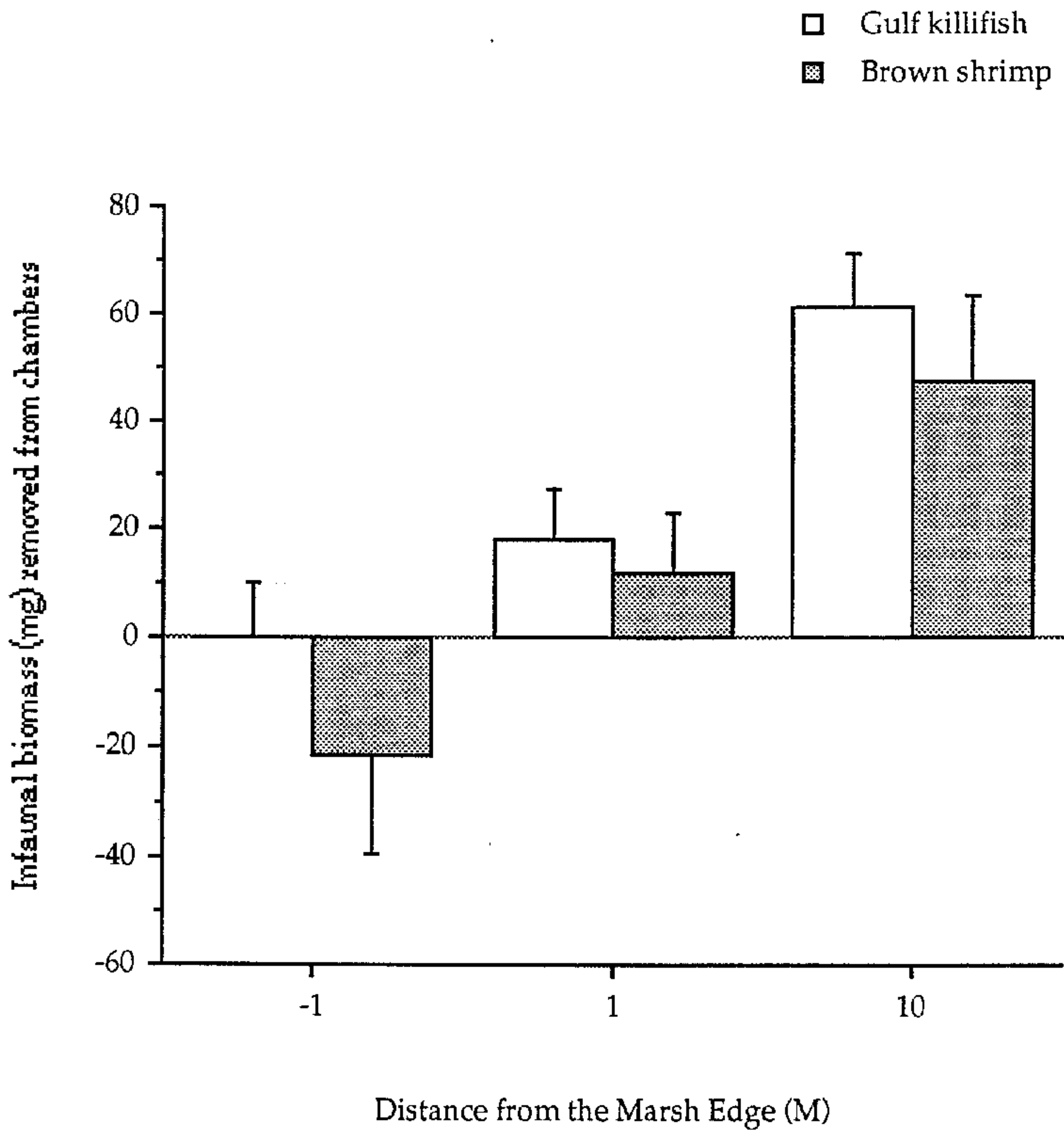
Figure 26 .   Mean infauna biomass (mg) removed by predators from experimental chambers during the spring experiment. Error bars represent one standard error.

1.2 mg/day. Over the 14 days, the mean increase in biomass for this species was 10.3%. Brown shrimp in control chambers with extra food had much higher growth rates averaging 56.1 mg/day (SE=4.45) and 1.0 mm TL/day (SE=0.07). There were no significant differences in growth measured in length or biomass among experimental microhabitats or predator species, but fed brown shrimp grew significantly faster than non-fed experimental shrimp (Table 14, Figures 27 and 28).

Infauna Removed from Sediments

Infauna from sediments in the summer experiment were again dominated by polychaetes (63% of total), and again the most abundant species were _Capitella capitata_, _Streblospio benedicti_, and _Laeonereis culveri_ (Table 15). Mean initial densities of overall infauna, annelids, _Streblospio benedicti_, and _Laeonereis culveri_ were similar to field densities observed eight days prior to the summer experiment (Figures 29 -32). However, both field and experimental infauna densities were reduced 70% compared with those in May (see Figures 17 and 29, Tables 11 and 15). In particular, crustaceans were extremely rare during August (mean densities were near zero in all microhabitats from the field collections in Chapter I, Table 15). Control densities of infauna were not significantly different among microhabitats (Table 14). When the number and biomass of prey removed by predators was analyzed for Microhabitat (Distance to Edge) effects, there were no differences in the number of infauna removed (Table 16, Figure 33). However, predators did remove a significantly higher biomass of infauna from the nonvegetated microhabitat compared to the edge microhabitat (Figure 34).

Table 14.   Analysis of variance results for growth of predators during the summer experiment. Growth was analyzed by daily change in length (mm, untransformed) and biomass (mg, square root transformation). *A priori* contrasts within the predator term were used to compare the growth of brown shrimp in experimental chambers to those in control chambers that were fed extra food, and the growth of each species of predator.

Length (mm):

Source	df	SS	MS	F	P
Distance to Edge (microhabitat)	2	0.079	0.039	1.358	0.2667
Predator	2	7.237	3.619	125.199	0.0001
Predator*Distance to Edge	4	0.091	0.023	0.784	0.5412
Residual	49	1.416	0.029		
Contrasts:					
Experimental brown shrimp vs. Control brown shrimp (fed)	1	5.727	5.727	198.153	0.0001
Experimental brown shrimp vs. White shrimp	1	0.003	0.003	0.112	0.7396

Biomass (mg):

Source	df	SS	MS	F	P
Distance to Edge (microhabitat)	2	7.559	3.780	1.138	0.3288
Predator	2	471.616	235.808	71.007	0.0001
Predator*Distance to Edge	4	630.557	3.670	1.105	0.3648
Residual	49	162.724	3.321		
Contrasts:					
Experimental brown shrimp vs. Control brown shrimp (fed)	1	394.913	394.913	118.918	0.0001
Experimental brown shrimp vs. White shrimp	1	0.686	0.686	0.207	0.6515

Figure 27 . Daily change in total length of brown shrimp and white shrimp in experimental chambers and brown shrimp in control chambers that were fed additional food over the 14 days of the summer experiment. Error bars indicate one standard error.

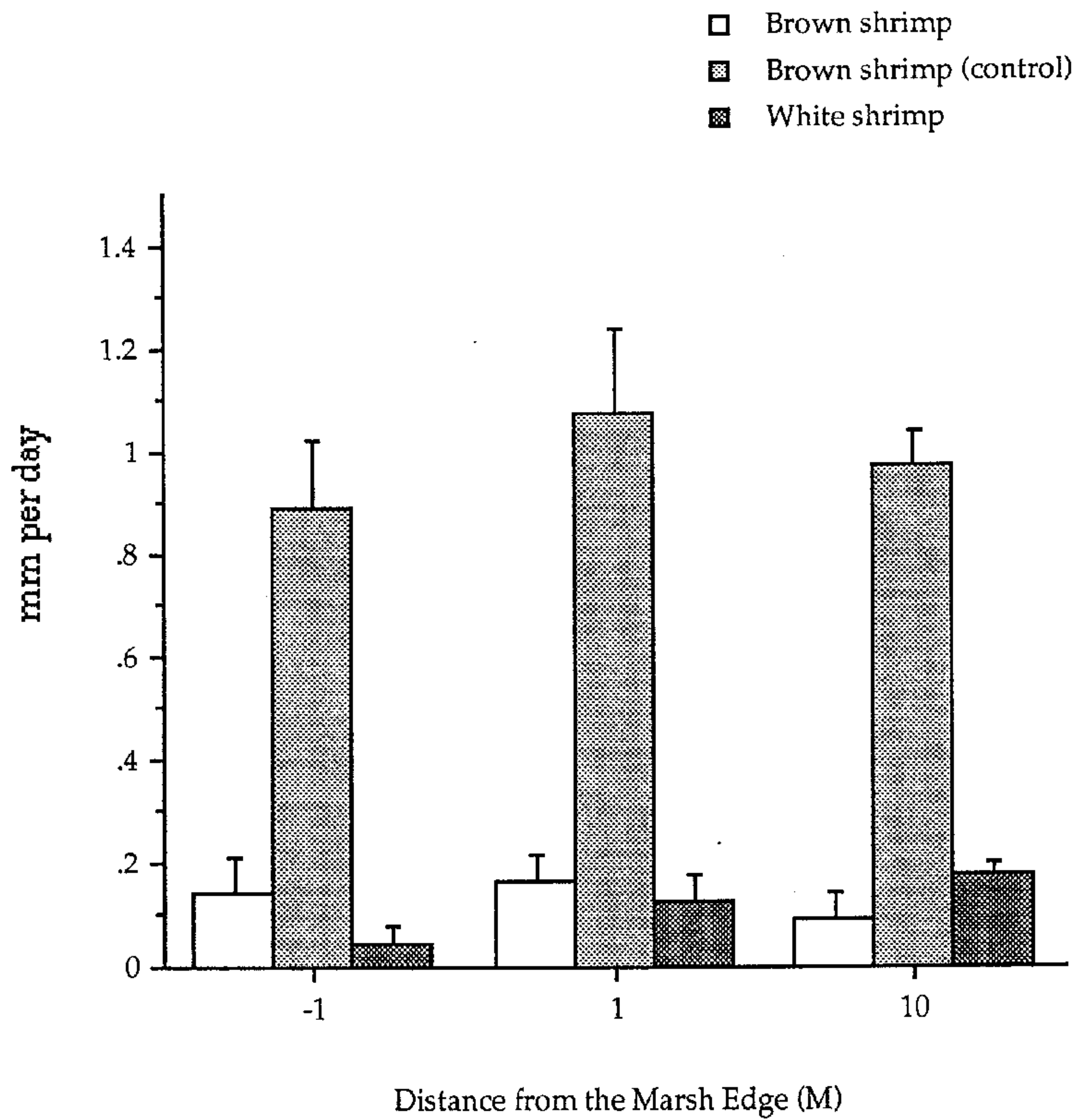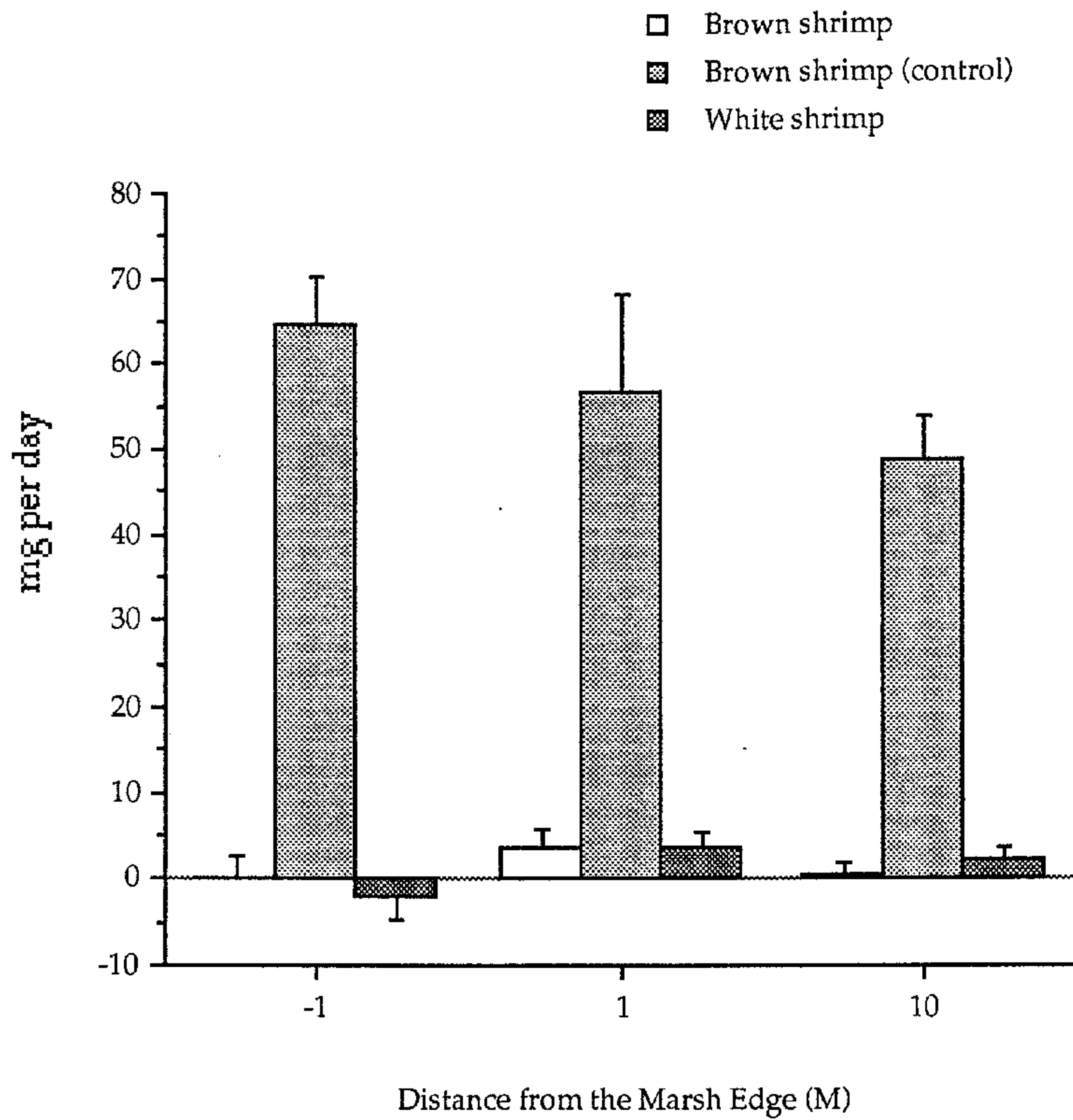Figure 28 .   Daily change in biomass of brown shrimp and white shrimp in experimental chambers and brown shrimp in control chambers that were fed additional food over the 14 days of the summer experiment. Error bars indicate one standard error.

Table 15.   Mean infaunal abundance and biomass (mg dry weight) values in control and experimental chambers in summer 1995 predation experiment (all microhabitats combined). Benthic infauna were sampled using a 19.6 cm^2 core and these numbers were extrapolated to mean number per chamber (323.6 cm^2, standard error is also shown). Control chambers contained no predators. Initial cores were collected when predators were placed into experimental chambers. Final control cores and experimental (with predator) cores were collected following the 14-day experimental period.

	Initial control (N=15)		Final control (N=15)		Brown shrimp (N=22)		White shrimp (N=23)	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Total Infauna	184.6	(37.57)	221.9	(33.62)	121.4	(39.88)	199.9	(24.31)
Annelida	181.3	(37.41)	210.9	(33.95)	119.9	(39.81)	198.5	(24.03)
Polychaeta	107.7	(30.16)	109.9	(20.88)	77.9	(31.15)	149.8	(15.91)
Capitella capitata	24.2	(12.03)	53.8	(16.81)	20.2	(13.18)	55.9	(5.52)
Streblospio benedicti	29.7	(11.04)	17.6.	(4.94)	30.7	(19.71)	58.0	(8.49)
Laeonereis culveri	42.8	(15.49)	30.8	(9.39)	26.2	(5.56)	25.8	(9.05)
Leitoscoloplos foliosus	6.6	(3.13)	2.2	(1.48)	0.7	(1.57)	2.1	(0.75)
Melinna maculata	1.1	(1.15)	3.3	(1.76)	0.0	(2.31)	3.6	(0.00)
Neanthes succinea	1.1	(1.10)	0.0	(0.00)	0.0	(1.69)	2.9	(0.00)
Mediomastus sp.	2.2	(1.48)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)
Eteone heteropoda	0.0	(0.00)	1.1	(1.15)	0.0	(0.72)	0.7	(0.00)
Polydora ligni	0.0	(0.00)	0.0	(0.00)	0.0	(0.72)	0.7	(0.00)
Sabella sp.	0.0	(0.00)	1.1	(1.10)	0.0	(0.00)	0.0	(0.00)
Oligochaeta	73.6	(28.51)	101.1	(22.41)	41.9	(11.37)	48.7	(17.30)

Table 15.   Continued

|	Initial control (N=15)		Final control (N=15)		Brown shrimp (N=22)		White shrimp (N=23)	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Crustacea	1.1	(1.10)	4.4	(1.95)	0.7	(0.72)	0.7	(0.75)
Hargeria rapax	1.1	(1.10)	3.3	(1.76)	0.0	(0.72)	0.7	(0.00)
Grandidierella bonnieroides	0.0	(0.00)	1.1	(1.10)	0.7	(0.00)	0.0	(0.75)
Mollusca	2.2	(1.48)	6.6	(2.69)	0.7	(0.72)	0.7	(0.75)
Acteocina canaliculata	2.2	(1.48)	5.5	(2.63)	0.7	(0.00)	0.0	(0.75)
Chione cancellata	0.0	(0.00)	1.1	(1.10)	0.0	(0.72)	0.7	(0.00)
Other	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)
Infaunal Biomass (mg)	68.9	(24.88)	40.5	(9.20)	23.8	(4.88)	44.5	(8.78)
Annelid biomass (mg)	68.9	(24.88)	40.5	(9.20)	23.8	(4.88)	44.5	(8.78)
Crustacean biomass (mg)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)
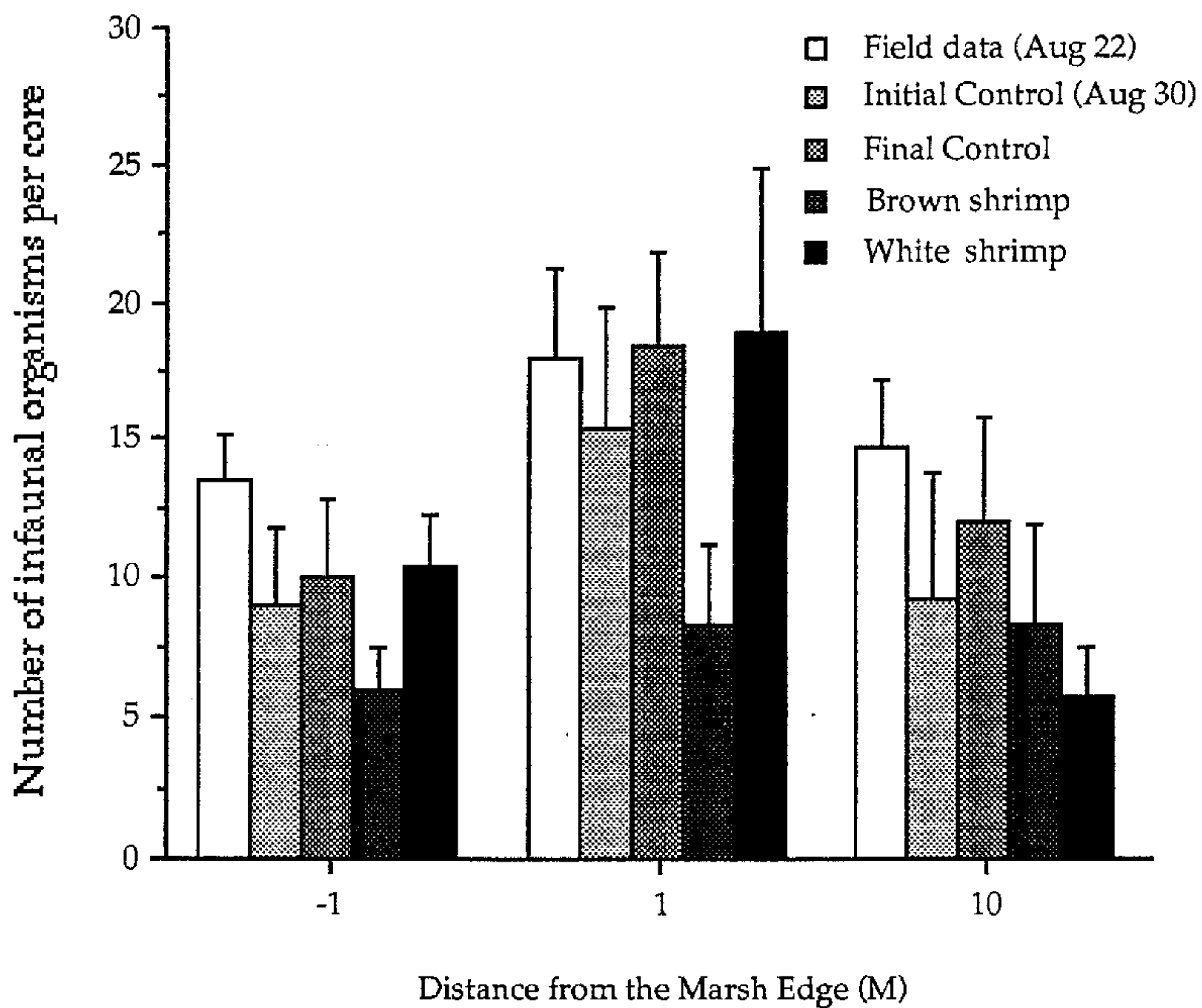
Figure 29.   Mean densities of infauna in three microhabitats
from sediment cores (N=25) taken from the marsh eight days prior
to the initiation of the summer experiment and in the control and
experimental chambers (see Table 9 for experimental Ns). Control
chambers contained no predators. Initial cores were collected when
predators were placed into experimental chambers. Final control
cores and experimental (with predators) cores were collected
following the 14-day experimental period. Each core had a surface
area of 19.6 cm^2 and a depth of 5 cm. Error bars represent one
standard error.

Figure 30.   Mean densities of annelids in three microhabitats
from sediment cores (N=25) taken from the marsh eight days prior
to the initiation of the summer experiment and in the control and
experimental chambers (see Table 9 for experimental Ns). Control
chambers contained no predators. Initial cores were collected when
predators were placed into experimental chambers. Final control
cores and experimental (with predators) cores were collected
following the 14-day experimental period. Each core had a surface
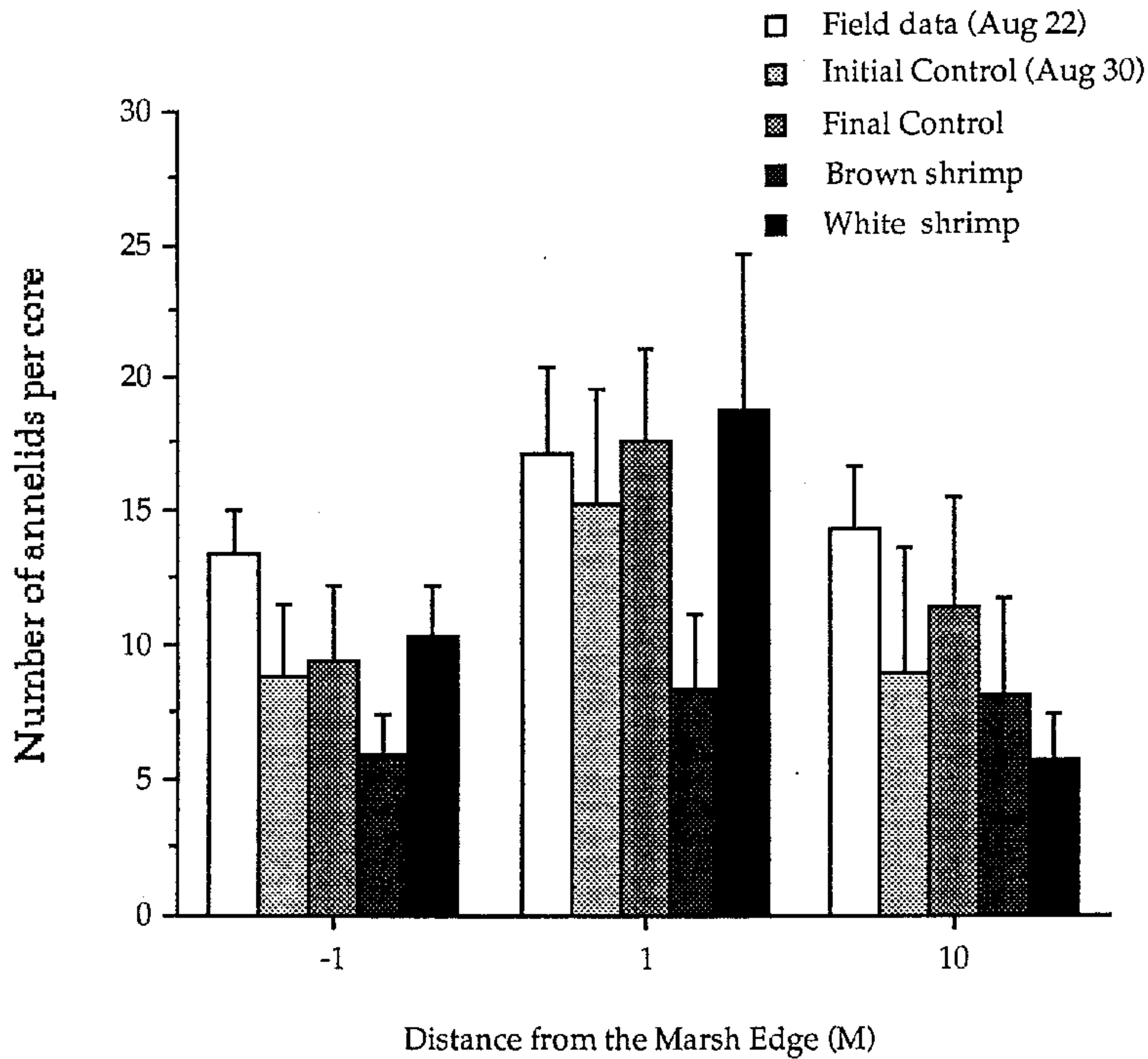area of 19.6 cm² and a depth of 5 cm. Error bars represent one
standard error.
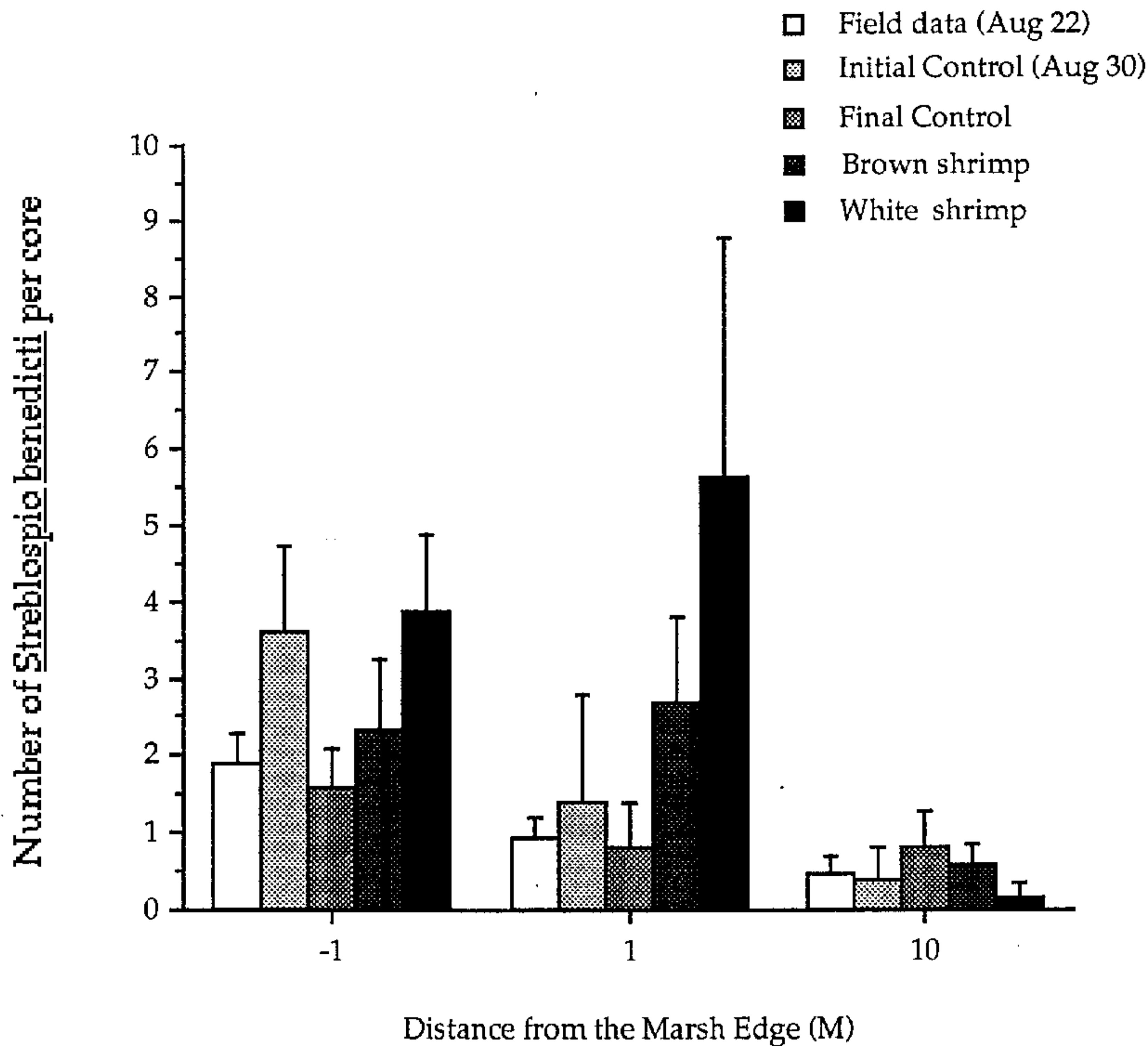
Figure 31.   Mean densities of Streblospio benedicti in three microhabitats from sediment cores (N=25) taken from the marsh eight days prior to the initiation of the summer experiment and in the control and experimental chambers (see Table 9 for experimental Ns). Control chambers contained no predators. Initial cores were collected when predators were placed into experimental chambers. Final control cores and experimental (with predators) cores were collected following the 14-day experimental period. Each core had a surface area of 19.6 cm² and a depth of 5 cm. Error bars represent one standard error.

Field data (Aug 22)
Initial Control (Aug 30)
Final Control
Brown shrimp
White shrimp

Number of Laeonereis culveri per core

Distance from the Marsh Edge (M)

Figure 32. Mean densities of Laeonereis culveri in three microhabitats from sediment cores (N=25) taken from the marsh eight days prior to the initiation of the summer experiment and in the control and experimental chambers (see Table 9 for experimental Ns). Control chambers contained no predators. Initial cores were collected when predators were placed into experimental chambers. Final control cores and experimental (with predators) cores were collected following the 14-day experimental period. Each core had a surface area of 19.6 cm^2 and a depth of 5 cm. Error bars represent one standard error.
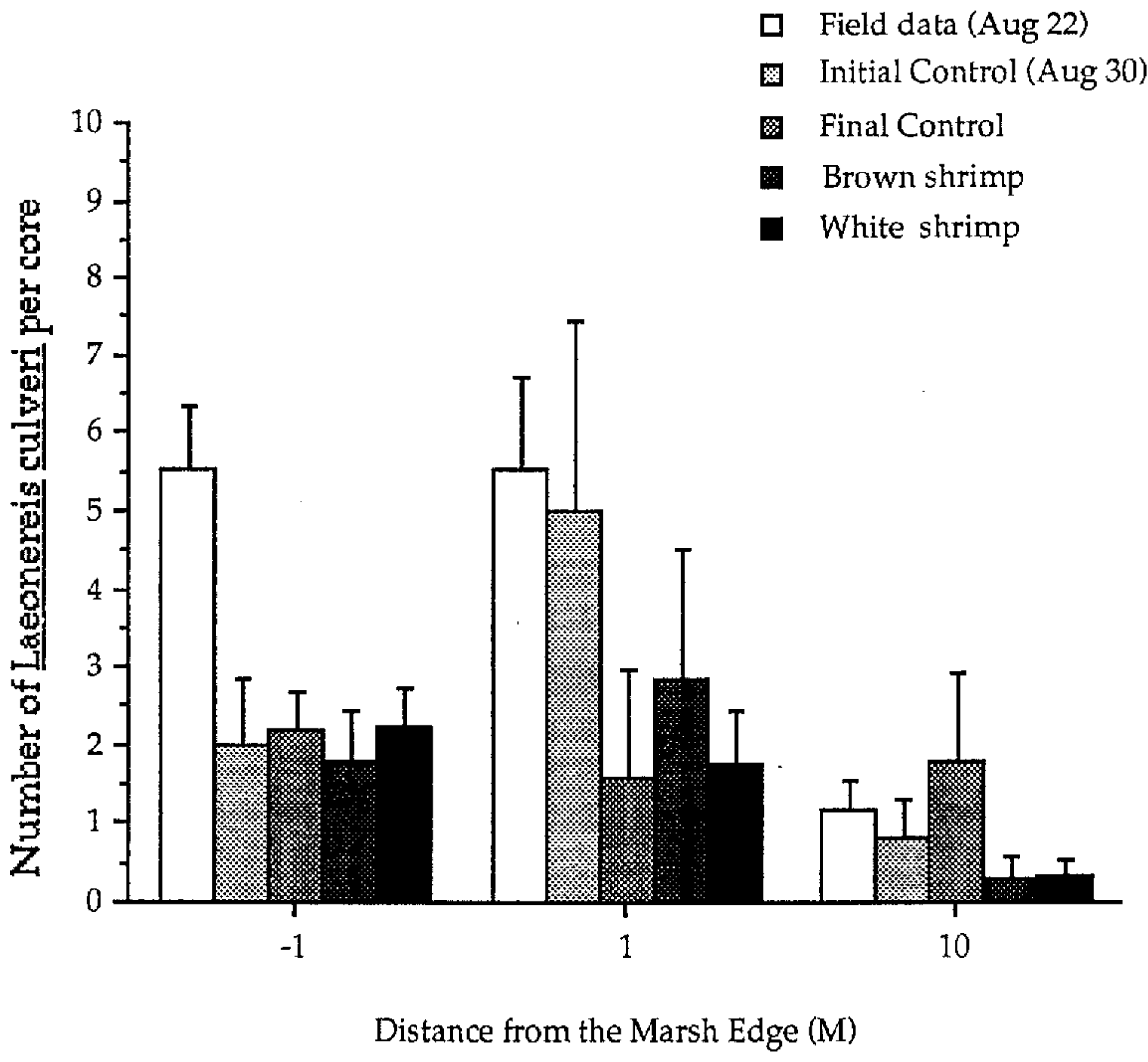
Table 16.   Results of two-way analysis of variance for number/biomass of infauna removed by predators in experimental chambers during summer 1995. *A priori* contrasts within the Distance to Edge (microhabitat) term were used to compare the number/biomass of infauna removed in the marsh edge microhabitat (1 M) to those in the nonvegetated (-1 M) and inner marsh (10 M) microhabitats.

Infauna   Abundance

Source	df	F	P
Distance to Edge	2	0.620	0.5431
Predator	1	2.184	0.1475
Predator*Distance to Edge	2	1.695	0.1969
Residual	39		

Infauna   Biomass   (mg)

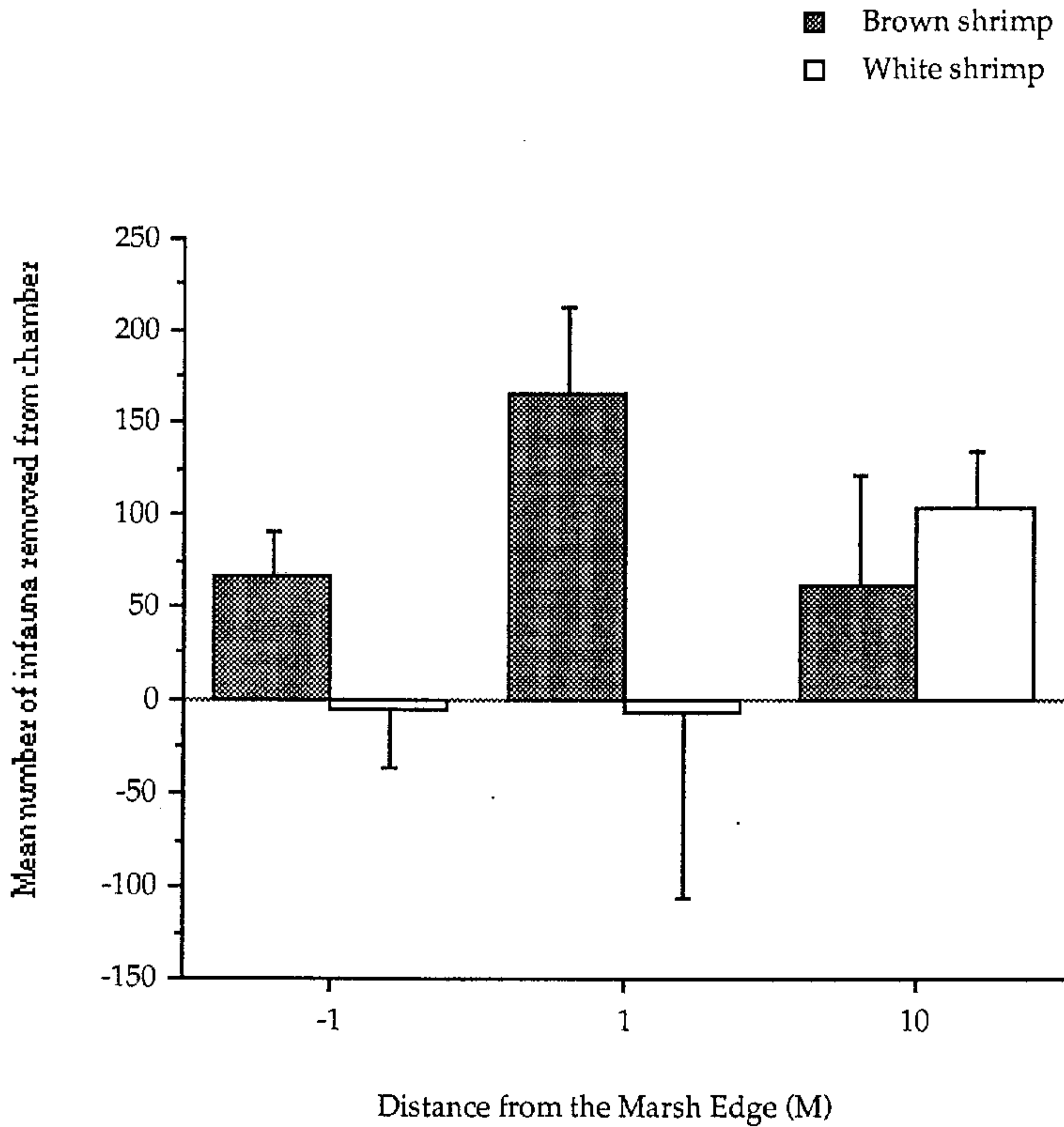| Source	df	F	P
Distance to Edge	2	6.944	0.0026
Predator	1	4.227	0.0465
Predator*Distance to Edge	2	2.688	0.0806
Residual	39		
Contrasts:			
-1 M vs. 1 M	1	12.201	0.0001
1 M vs. 10 M	1	0.529	0.4720

Figure 33.   Mean number of infauna removed by predators from experimental chambers during the summer experiment. Error bars represent one standard error.
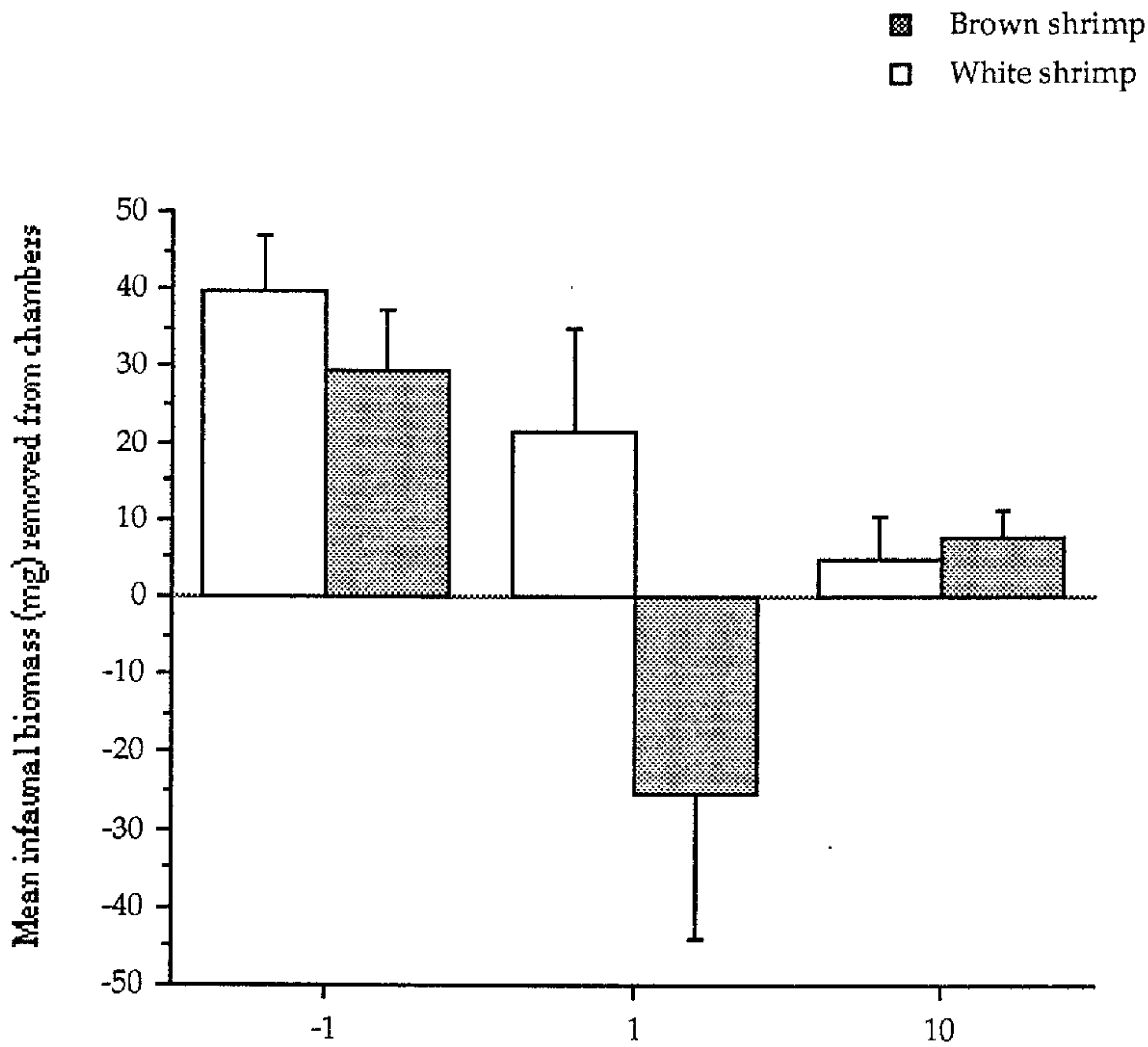
Figure 34.   Mean infaunal biomass (mg) removed by predators from experimental chambers during the summer experiment. Error bars represent one standard error.

Discussion

In this experimental study, I brought marsh sediments from three different microhabitats into the laboratory to examine the relative value of associated infaunal communities as sources of food for several common marsh predators. Studies have shown that marsh sediments provide an important food source to many nektonic predators (Fritz 1974; Kneib and Stiven 1978; Weisberg and Lotrich 1982; Zimmerman et al. 1991). However, the relative value of microhabitats within the marsh has not been extensively studied. The predators examined in this experimental study are among the most abundant nekton present in salt marshes of the Gulf of Mexico (Zimmerman and Minello 1984; Peterson and Turner 1994), and the timing of my experiments was designed to match peak abundances of these predators. Abundances of brown shrimp in western Gulf of Mexico estuaries generally peak in the late spring and early summer, and juvenile white shrimp peak in the summer and fall (Baxter and Renfro 1966; Copeland and Bechtel 1974; Zimmerman and Minello 1984). Gulf killifish reside in marshes throughout their life cycle and abundances peak in summer (Lipcius and Subrahmanyam 1986).

The predator species used in my experiments have been shown to feed on benthic infauna found in salt marsh sediments (Rozas and LaSalle 1990; Minello and Zimmerman 1991). In my field study, I found that during much of the year, infauna densities in the marsh edge microhabitat were significantly higher than in other marsh microhabitats (3, 5, and 10 M from marsh edge) and nonvegetated habitats one meter downslope of the marsh edge (-1 M). Many predators have also been found to concentrate on the marsh edge even when extensive intertidal marsh is available at high

tide (Baltz et al. 1993; Kneib and Wagner 1994; Minello et al. 1994; Peterson and Turner 1994). These predation/growth experiments were performed to determine if higher abundances of infauna on the marsh edge translate into higher growth rates for predators using this microhabitat.

Growth rates for the predators in both experimental trials were substantially lower than natural rates reported in the literature. Growth rates for juvenile brown shrimp and white shrimp while in the estuary are approximately 1 mm per day (Minello and Zimmerman 1991). My laboratory growth rates were 0.1 and 0.2 mm per day for brown shrimp and 0.1 mm per day for white shrimp. Gulf killifish did not grow in the experiment and lost around 13% of their body weight over the two-week experimental period. Fundulus heteroclitus, a species very similar to Fundulus grandis, has been estimated from field studies to increase an average of 4.4% of its total weight per day in natural conditions (Kneib and Stiven 1978).

Growth rates of the three species did not differ among marsh microhabitats in either the spring or summer experiment. Growth rates among predators did vary during the spring experiment, where brown shrimp had significantly higher growth rates than gulf killifish. During the summer experiment, growth rates of brown and white shrimp were not significantly different.

The lack of differences in growth among microhabitats may be explained by similarity in initial densities of infauna in experimental chambers; control densities were not significantly different among the microhabitats for either experiment. Information on seasonal abundances in the microhabitats obtained from my field study suggest that low densities

of infauna throughout the marsh may be a seasonal occurrence in August. However, results from this same field study show that densities of infauna are consistently highest on the marsh edge compared to nonvegetated and inner marsh microhabitats (-1 M and 10 M) throughout the spring and especially during May (Figure 2). Densities of infauna on the marsh edge were reduced to densities similar to those at the nonvegetated and inner marsh (10 M) microhabitats between the field collection on May 12 and when the experiment began on May 24 (Figure 17). Removing the sediment cores from the marsh edge and placing them in a water table may have removed whatever advantage the marsh edge has for infaunal species, thus causing the reduction in infauna density.

All predators examined removed substantial numbers and biomass of infauna from experimental chambers, but available sediments did not provide sufficient infaunal prey to maintain natural growth rates. Differences in the number and biomass of infauna removed among microhabitats did not translate to significant differences in growth rates. When additional food was added, brown shrimp growth rates increased significantly and approached natural rates. These data indicate that growth was food-limited in the experimental chambers. Therefore, growth rates may not have been an accurate measure of microhabitat value.

CHAPTER V

CONCLUSIONS

Infaunal densities within marsh vegetation were highest one meter from the marsh edge compared with densities farther from the edge during most of 1995 in Gang's Bayou. Distributions of surface-dwelling infauna had the strongest relationship with marsh edge, whereas some subsurface feeders were not affected by proximity to marsh edge. Infaunal abundance was related to elevation only during the early spring, mid-summer, and late fall when inundation times were low or variable. These data suggest that edge effects are often more important than elevation effects in controlling ecological factors that affect infaunal distributions within the salt marsh. More research is needed to determine the mechanisms by which marsh edge affects abundances of surface-dwelling infauna.

Marsh sediments are valuable to many species of nekton as an important food source. The relative value of sediments in salt marsh microhabitats, however, remains unknown. Predators foraging on marsh sediments in experimental chambers were unable to maintain natural growth rates, and were probably food-limited. As a result, growth rates for brown and white shrimp, and gulf killifish were not significantly different among microhabitats. All three predators did remove substantial numbers and biomass of infauna from the chambers, but apparently not enough to maintain natural growth rates. In addition, infauna densities within the edge chambers in the May experiment probably did not represent natural conditions. Infaunal densities in the edge chambers were reduced compared to those found on the marsh edge two weeks prior to the experiment. Because both predator growth and infaunal densities did not represent

natural conditions, the relative value of microhabitats could not be determined.

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VITA

Shannon DiAnn Whaley
4109 Vista Blvd.
Galveston, TX 77554

B. S., Marine Biology, Texas A&M University, College Station, TX,
December, 1992.

Professional Societies: Estuarine Research Federation,
                                 Society of Wetland Scientists

Experience:

February 1997 - present
Benthic Ecology Laboratory Manager, National Marine Fisheries
Service, NOAA, Galveston Laboratory, Fishery Ecology Branch

September 1996 - February 1997
Graduate Assistant - Non-teaching, Texas A&M University at Galveston,
Marine Biology Department

February 1995 - December 1996
Expert taxonomist on benthic infauna, Whaley Environmental and
Ecological Consulting. President and owner.

September 1994 - January 1995
Graduate Assistant - Teaching (Microbiology and General Biology Labs),
Texas A&M University at Galveston, Marine Biology Department

December 1992 - February 1995
Fisheries Biologist, National Marine Fisheries Service, NOAA, Galveston
Laboratory, Fishery Ecology Branch

October 1992 - December 1992
Biological Aide - Student Appointment, National Marine Fisheries
Service, NOAA, Galveston Laboratory, Fishery Ecology Branch